STABILITY IN AN ASSEMBLAGE OF CARIDEAN AND PENAEID SHRIMPS INHABITING AN INTERTIDAL *THALASSIA* BED

By

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For my Mother and Father

with Love and Respect

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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Fourteen species of caridean and penaeid shrimps were collected during 27 months of sampling in an intertidal Thalassia bed adjacent to Seahorse Key, Florida. This assemblage was found to be resilient following annually occurring episodes of seagrass blade shedding. Stability was evaluated through three techniques which used differing combinations of the information types available in a species by sample (collection date) data matrix. The finding of stability suggested that deterministic processes controlled assemblage structure.

Hippolyte zostericola, a small hippolytid, was numerically dominant in 26 of the 27 monthly samples and it was the only species present in all samples. Total and relative abundances of each of the 14 species greatly fluctuated through time. Changes in population size for most species were positively correlated with annual cycles of change in the above ground biomass of seagrasses. The assemblage was

found to be resilient despite broad and mostly irregular changes in species abundances. An uneven distribution of individuals among the assemblage members and consistently occurring separation of yearly abundance peaks among the Hippolytidae provided circumstantial evidence that interspecific interactions might regulate assemblage structure.

None of the small carideans were found to be detritivores. The hippolyitds were micrograzers on algae epiphytic on seagrass blades and the palemonids included an omnivore and a strict carnivore. An SEM examination of their feeding appendages reinforced these findings. Ecological similarity of the hippolytidae was observed in patterns of body size, in seasonal patterns of brooding and recruitment, and in field-determined patterns of feeding activity. Competitive interactions between species were speculated to have contributed to the resilience observed in this grassbed assemblage.

CHAPTER I
GENERAL INTRODUCTION

The structures of ecological assemblages are known to be dependent on a continuum of controlling mechanisms. Most multispecies assemblages seem to be organized by some combination of stochastic and deterministic processes. Certain communities, however, seem to lie closer to one end of this continuum than to the other. Coral reef fish assemblages, for example, are largely dependent on unpredictable changes in the supply of living space (Sale, 1977). In contrast, the spatial distributions of barnacles in some fouling communities are primarily determined by interspecific competition for living space (Connell, 1961). Even in these seemingly distinct cases, community dynamics are affected by both randomly occurring events and by deterministic processes (Sale, 1977; Grossman, 1982; Grossman et al., 1982).

Theory relating to community structure is, at present, biased towards deterministic processes due to the assumed importance of interspecific competition. This assumption is largely based on observations of competitive interactions between vertebrates (reviewed by Lawlor and Strong, 1981). In insect assemblages these two authors found that strong interspecific interactions are too rare to have a great effect on community structure.

Ideas concerning structural regulation in seagrass communities vary greatly among authors. Several researchers (Coull and Bell 1978; Heck and Orth, 1980) have assumed the high concentrations of detritus found in seagrass meadows obviate the importance of food-based competition as an important community regulating process. Gore et al. (1981) suggested that the resilient structure of an assemblage of seagrass meadow-dwelling decapod crustaceans may have been due to competition for food resources. Coen et al. (1981) and Thorp (1976) demonstrated that competition for preferred habitat types may play a role in structuring decapod assemblages. Predation is generally assumed to have the largest role in structuring assemblages in this predator-rich environment (Howard, 1981; Leber,1983).

As noted in Grossman et al. (1982) direct tests of community regulating mechanisms are rare due to the logistical and ethical problems involved in perturbing sufficiently large areas of natural communities. Natural perturbations can be utilized as "experiments" to determine the resilience of community structure (i.e. Dauer and Simon, 1976; Santos and Bloom, 1980). If a community is found to be resilient after a perturbation then it can be assumed that deterministic processes control the structure of the community (Grossman, 1982; Grossman et al., 1982; Moyle and Vondracek, 1985).

Annually occurring fluctuations in both the biomass of the seagrass Thalassia testudinum and in the abundances of 14 shrimp species served as a natural experiment to test

concepts relating to the control of structure in a macrofaunal assemblage. In the northeastern Gulf of Mexico seagrasses undergo annual cycles of blade-shedding and subsequent regrowth. Defoliation reportedly occurs when temperatures drop below 20°C or rise above 30°C (Phillips, 1960; Zieman, 1982). Partial defoliations may also occur after extended periods of blade exposure during low spring tides (Zieman, 1982). At Seahorse Key, Florida, low temperature blade-shedding is almost complete in shallow-water seagrass beds (Reid, 1954; Thursby, 1976; personal observation). These annual defoliations result in substantial reductions in species abundances and in species richness among the resident assemblage of caridean and penaeid shrimps (Vann, 1980; personal observation). Seagrass-associated fishes are similarly affected (Reid, 1954) and the total density of the benthic infauna also undergoes a seasonally evident pattern of change (Bloom, 1983).

When water temperature increases in spring new blades are produced on the short-shoots which branch from turtle grass rhizomes (Zieman, 1982). During periods of high blade biomass seagrass associated macrofauna are beneficially affected by the increased structural complexity through a variety of mechanisms. These effects include: 1) protection from predators (Heck and Wetstone, 1977; Heck and Orth, 1980; Heck and Thoman, 1981; Coen et al., 1981), 2) increased substratum for growth of epiphytes (Humm, 1964; Reyes-Vasquez, 1970; Thursby, 1976) which are consumed by

micrograzers (Morgan, 1980; Orth and Van Montfrans, 1984; Kitting et al., 1984), 3) protection from temperature stress and dessication in shaded microhabitats (Zieman, 1982), 4) increased sedimentation of inorganic and organic particles (Zieman, 1982), and 5) reduction of current velocity on the surface of underlying sediments (Dawes, 1974; Zieman, 1982). Thus, significant losses of seagrass blades should result in increased stress, through these mechanisms, on the motile macrofauna found in seagrass meadows.

I examined patterns of shrimp species abundances over a 27-month sampling period (Chapter II) to 1) document population cycles of each species, 2) to document several aspects of the life history and size patterns of the more abundant species, and 3) to determine if the shrimp assemblage demonstrated characteristics of a deterministically or a stochastically regulated community. Chapter III presents the results of a study of trophic and behavioral interactions which were thought to be important in regulating community structure.

CHAPTER II
POPULATION PATTERNS AND COMMUNITY STABILITY

Introduction

At Seahorse Key, Florida, severe disturbances in the structure of shrimp assemblages follow annually occuring episodes of seagrass blade shedding in low-intertidal grass-beds. Patterns of shrimp species abundance in this habitat were followed through 27 months of sampling. The population patterns were then subjected to three methods of stability assessment in order to determine the nature of processes which might control assemblage structure in this group of shrimps.

Methods of analysis of community stability in marine communities include observation of population patterns over multiyear cycles (Livingston et al., 1975), the use of indices of community stability (Petersen, 1975; Coull and Fleeger, 1977), cycling in similarity indices (Heck, 1977), classification analysis (Boesch, 1973; Coull and Fleeger, 1977; Bloom, 1983; and many others), measurements of the stochastic boundedness of diversity indices (Kay and Butler, 1983), and concordance analyses (Grossman et al. 1982; Moyle and Vondracek, 1985). This listing is not complete but it does show the diversity of methods currently used in stability assessments. Among the techniques listed, the

concepts of stochastic boundedness and of community concordance include statistical tests of stability. Stochastic boundedness is, however, only applicable to communities which show a lack of change through time. Concordance analyses are applicable to systems which experience perturbations in community structure but are limited in that Kendall's measure of concordance (Siegel, 1956) considers only species' identities and their ranked abundances.

Bloom (1980) proposed, tested, and later used (Santos and Bloom, 1980) an objective method of appraising the resilience of a community. The technique Bloom developed utilizes, as do other multivariate techniques, all of the information available in a data matrix (Bloom, 1980). The technique uses information on the numbers of species and their abundances while keeping track of their identities. Additionally, it includes a geometrical and hypothesis-testing statistical analysis as described in Bloom (1980). The basic technique closely conforms to the concept of stability defined as resilience by Holling (1973).

The Bloom measure can be applied to communities which undergo a significant natural or man-caused perturbation in community structure. It requires an adequate description of the pre-perturbation or base-line community and that the "recovery" be monitored for a reasonable length of time. Santos and Bloom (1980) monitored the recovery of a benthic community which was subjected to annual mid-summer episodes of hypoxia. This short-lived stressor resulted in a total dieoff of the benthic infauna at their station in Tampa Bay,

Florida. Although the annual seagrass defoliation at Seahorse Key did not result in total defaunation and was not as temporally well-defined as the hypoxic conditions described in Tampa Bay, Bloom's technique was considered appropriate to determine the resilience of the shrimp assemblage inhabiting these seagrass beds. In addition to using the method developed by Bloom, dendrograms from classificiation analyses and a concordance analysis were also used in assessing the stability of this shrimp assemblage through time.

Stability (defined as the ability to return to a certain pre-perturbation species mix) implies some level of organization in a community. It thus becomes important to determine if the organization in a stable community is due to 1) inherent life history traits of the component species, 2) interactions of species with the abiotic environment, and/or 3) biological interactions between species. Strategies that species might follow in a resilient community include several life history and ecological traits (Orians, 1975; Moyle and Vondracek, 1985) which can be determined from sampling studies, e.g. generation times and feeding patterns.

In relation to density-dependent phenomena, sampling studies and natural experiments have certain weaknesses that have been widely discussed. Often, however, manipulative experimentation on a large-scale basis is not possible (cf. McGowan and Walker, 1979; Joern and Lawlor, 1980) or creates such a high level of artificiality that its results are meaningless. Manipulative experiments conducted in seagrass

and other soft-bottom communities suffer from a wide range of problems (Virnstein, 1978; Leber, 1983) which, in some cases, cannot be resolved.

A further problem with successful manipulative experimentation is that results indicating the presence of deterministic mechanisms (e.g., competition or predation) do not exclude the possibility that the community is more strongly influenced by stochastic events. Experimentation and/or close observation of pattern should be coupled with long-term monitoring of individual population fluctuations to understand the interactions of deterministic and stochastic processes in determining community structure.

Correlative techniques and other methods of comparison, were used here to attempt to explain the stability observed in this shrimp assemblage through autecological studies of its component species. These observations centered on the population dynamics and several life-history traits of seven, small caridean species. As a group they comprised a high percentage of the total number of individuals present in the grassbed throughout this study. Patterns of reproduction and recruitment, overlap in size, and changes in size-frequency distributions were compared among species to determine factors which might influence coexistence and regulate assemblage structure within this caridean-dominated (Vann, 1980) shrimp community.

Methods

Study Site

The study area was established in the seagrass beds adjacent to Seahorse Key, Florida (83° 04' West and 29° 06' North). Seahorse Key (Figure 2-1) is one of the Cedar Keys and is located 5 kms southwest of the town of Cedar Key. The Cedar Keys area is approximately 145 kms north-northwest of Tampa, Florida.

Seagrasses in this area include Thalassia testudinum Banks ex Konig (turtle grass), Syringodium filiforme Kutz (manatee grass), Halodule beaudetti (den Hartog) (shoal grass), and Halophila engelmanni Ascherson. Humm (1964) listed the many species of Thalassia epiphytes found in Florida waters. A site-specific listing of Thalassia epiphytes was given by Thursby (1976).

The seagrass beds adjacent to the southern and eastern shores of Seahorse Key show a definite zonation pattern which is characteristic of the seaward-most islands in the Cedar Keys (Maden, 1978; Bloom, 1983; Hicks, 1983; personal observation). Reasons for patterns of seagrass zonation have been addressed in general by denHartog (1977) and specifically for Seahorse Key by Bloom (unpublished manuscript). At Seahorse Key a narrow band (10-12m wide) of open, muddy sandflat extends seaward from the lower edge of the coarser grained upper beach. A second narrow band consisting of Halodule extends seaward 40 to 50 m beyond the sandflat. In most places the Halodule bed ends abruptly in

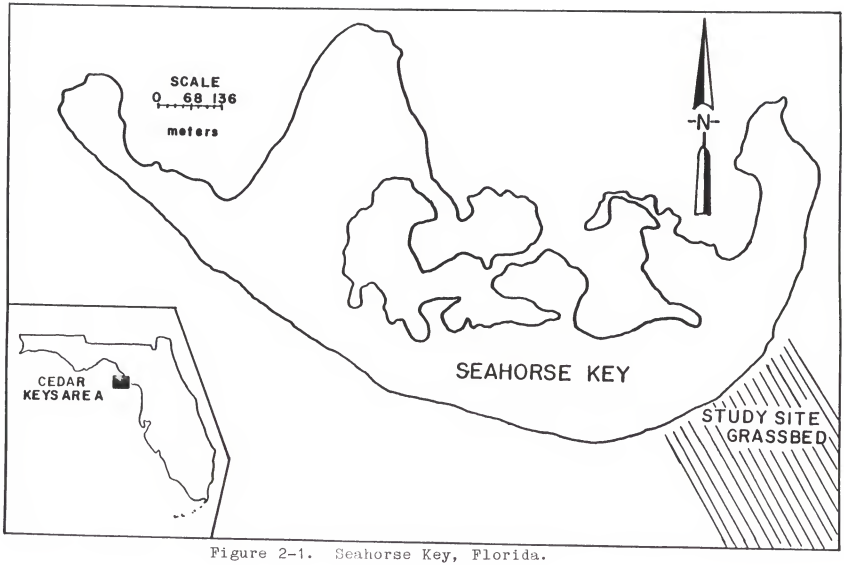


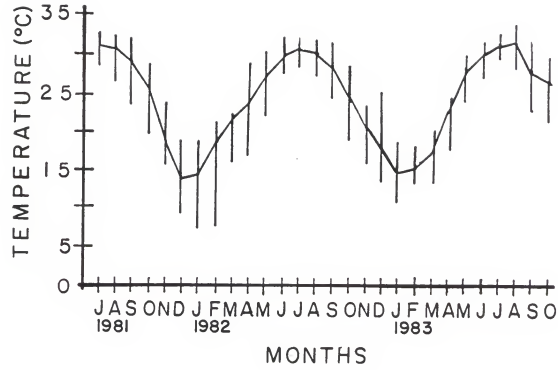
Figure 2-1. Seahorse Key, Florida.

a large, almost monospecific bed of short-bladed Thalassia. Small patches of shoal grass and manatee grass are irregularly interspersed within this turtle grass flat.

At the extreme outer edge of the Thalassia bed there is a gradual change to a mixed bed of longer-leaved turtle grass and Syringodium. Halophila is present but uncommon in this bed of mixed seagrass species. Attached and drifting macroalgae seem to be most abundant in this outer zone. On the eastern side of Seahorse Key the outer band of seagrasses continues up to the edge of the ship channel leading into Cedar Key. Seagrass beds on the south side of the island extend seaward for several kilometers until they end in deep water.

As mentioned in Chapter I seagrasses in shallow water at Seahorse Key are highly seasonal in above ground biomass. Roots and rhizomes of Thalassia survive the winter at Seahorse Key but above ground blade biomass approaches 0 g/m^2 (Thursby, 1976; Vann, 1980; personal observation). An annual cycle of defoliation and leaf regrowth is reported and discussed later in this chapter.

Salinity in the Cedar Keys area is strongly influenced by seasonally heavy outflows of the Suwannee River (24.1 kms to the north-northwest) and the Wacassasa River (19.3 kms to the east). Salinity, as observed at a NOAA station located on the city dock in the town of Cedar Key, ranged from 2.4 to 34.5 $^{o}/_{oo}$ during this study. Temperature at this same station varied from 7.2°C to 33.3°C. Monthly means and ranges of salinity and temperature are shown in Figure 2-2.



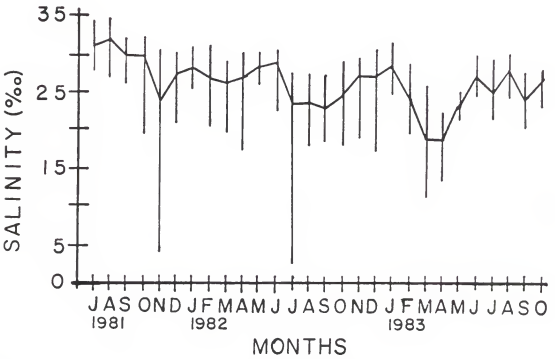


Figure 2-2. Temperature and salinity means, as recorded at the NOAA station in Cedar Key, Florida, from July 1981 through October 1983. Vertical lines represent monthly ranges.

A high/low recording thermometer, in place at the study site from August 1982 through September 1983, recorded a low of 6.7° C and a high of 36.7°C. The thermometer was shallowly buried and its recordings were probably slightly buffered by the insulating effect of sediments and seagrasses.

Monthly Sampling Program

An epibenthic sled was used to collect shrimp at the primary study site at approximately monthly intervals from August 1981 to October 1983. The sled was pulled at slow speed along a marked 25m course. The sled frame was rigid and measured 0.5m in width and 0.45m in height. The bottom area sampled in each sled haul was approximately 12.5m^2. Six replicate hauls were usually taken on each sampling date. Severe net damage on three dates resulted in completion of less than the usual number of sled hauls.

The sled was equipped with a fiberglass screen bag of 1.2mm mesh. This net efficiently captured all but the smallest size classes of most shrimp species. This mesh was chosen after discovering that bags with smaller mesh sizes rapidly filled with sand. The sled was heavily weighted (30kg) with steel rods in the PVC runners. A thin aluminum blade was fastened to the lower, leading edge of the sled box. The sled frame, and thus the blade, was set at a forward-sloping angle. These design features were intended to increase the sled's catch efficiency.

All sled hauls during the 27 months of sampling were taken on the eastern edge (Fig. 2-1) of the large Thalassia

flat which surrounds Seahorse Key. This site seemed similar to the rest of the nearshore turtle grass bed in that it was very sandy and was covered by short-bladed Thalassia. The sampled area was chosen due to its accessibility during low tides. Course markers were moved slightly each month to avoid resampling recently sampled areas. All sled tows were made during or near daytime high tides. If the tide was flowing the sled was pulled against the direction of tidal flow.

Salinity and water temperatures were measured at the start of each month's sampling. Salinity was measured with either a portable salinometer or a refractometer. From December 1982 to October 1983 the combined biomass of seagrasses and their epiphytes were determined from core samples. Six cores of $0.18m^2$ each were taken during early seagrass sampling. The number of samples was increased to 11 per month during the last eight months of the sampling program.

Upon collection all shrimp samples were preserved in $NaHCO_3$ buffered, 10% formalin in seawater. Seagrass samples were placed on ice. Seagrass blades in each replicate were separated from their roots and bases, wrapped in preweighed, perforated sheets of foil, dried in a forced air drying oven at $80^{o}C$ for one week, and then reweighed. In the laboratory shrimp were separated from mats of seagrass and algae by hand picking and by the use of an elutriation device. This device helped in speeding up an otherwise very slow, tedious job. It also reduced the sorter's exposure to

formaldehyde. After rough sorting all shrimp samples were preserved in either 50% isopropanol or 70% ethanol. Prior to identification and counting the larger samples were split in a Folsom plankton splitter. Preliminary tests of the splitter for possible effects of the relatively large size of caridean shrimp showed that it worked correctly. The actual number of individuals counted from split samples always exceeded 150 shrimp and, in all but three cases, exceeded 200 individuals per replicate sample.

Density Estimates

The catch efficiency of the epibenthic sled was determined in order to convert sled catch data to more accurate estimates of field densities. Sled catch efficiencies were determined by dipnetting shrimp from seven $0.25m^2$ cages, randomly placed in the primary sampling area. The enclosed bottom and cage sides were repeatedly swept with the dipnet until no shrimp were captured in several consecutive sweeps. Dipnetting usually resulted in almost total defoliation of the sampled areas and was considered to be highly effective. The mesh in the dipnet and in the cage sides was the same mesh used in the bag of the epibenthic sled.

The density of shrimp determined from the cages was compared to a density value estimated from a series of seven sled tows over a 25m marked course. This procedure was repeated twice and the catch efficiency values from the separate trials were averaged. Average values were then used to convert raw catch data into density estimates.

During the first trial very few species were present on the grass flat and thus the conversion factors for most species were based on data from the second trial.

Size-Frequency Analyses

Up to 160 shrimp of each species were measured from combined monthly replicate samples. For use in interspecific comparisons, carapace lengths were converted to total lengths through regression equations (Table 2-1). Size-frequency histograms were constructed from these data for four of the five most abundant shrimps. Densities of juvenile shrimps (defined here as the two smallest size classes of each species collected during the entire study) and of brooding females were estimated from the total densities of all seven species in all monthly samples. Hutchinsonian ratios (Hutchinson, 1959) were determined using mean size data for each population and for embryo-carrying females of each species.

Stability Analyses

Population counts from monthly collections were analyzed further by a statistical package designed specifically for community data (Community Analysis System, Ecological Data Consultants, Inc.). This set of programs, used on a microcomputer (Apple IIplus), calculates various sample characteristics, i.e. the number of species, density (if appropriate), various measures of diversity, and evenness. It also ranks species by their abundances and gives the

Table 2-1. Regression equations used to determine total lengths from carapace lengths. The numbers of individuals measured (N) and r^2 values are shown with each equation.

Hippolyte zostericola: ($N = 100, r^2 = 0.95$)

$Y = 0.617 + 3.63\ X$

Tozeuma carolinense: ($N = 100, r^2 = 0.98$)

$Y = -4.49 + 3.40\ X$

Thor dobkini: ($N = 60$, $r^2 = 0.92$)

$Y = 0.190 + 4.12\ X$

Latreutes fucorum: ($N = 114$, $r^2 = 0.95$)

$Y = -0.094 + 3.25\ X$

Latreutes parvulus: ($N = 52$, $r^2 = 0.93$)

$Y = 0.440 + 2.76\ X$

Periclimenes americanus: ($N = 114$, $r^2 = 0.95$)

$Y = 0.613 + 3.16\ X$

Periclimenes longicaudatus: ($N = 100$, $r^2 = 0.83$)

$Y = 0.704 + 4.41\ X$

number of months in which each species was present during the sampling program. Additionally, it analyzes data matrices to produce classification analyses. In this study matrices using both log ($\log_{10}(n + 1)$) and frequency transformed data were analyzed with Czekanowski's Quanitative Index to produce similarity matrices. Group-average and flexible sorting were used as classification schemes to produce dendrograms. The resulting dendrograms were used to judge the presence or absence of repeating patterns in the changing composition of the caridean faunal component in this seagrass community.

Techniques developed by Bloom (1980) and later used by Santos and Bloom (1980) were utilized to help determine if the seasonal patterns seen among the shrimp species in this community were stable through time. A matrix with species as rows and collection dates as columns was constructed from monthly sled haul data. Data, as used in the matrix, were sled haul counts converted to density values on a per square meter basis. Densities were log transformed, as shown above, prior to further analysis.

The log transformed data matrix was subjected to principal coordinates ordination analysis which extracts the eigenvalues (latent values) of the matrix. The analysis is limited to the first three eigenvalues derived from the matrix. The eigenvalues of all of the initial pre-perturbation samples were then plotted in an n-dimensional system with the eigenvalues as cartesian coordinates. The pre-perturbation coordinates are used to define a space. As

described in Santos and Bloom (1980), a 95% confidence polygon in three dimensions is constructed around the pre-perturbation space. Each post-perturbation sample is sequentially plotted, using its eigenvalues as coordinates, to determine if it enters the 95% confidence envelope around the pre-perturbation cluster. Samples which do enter the confidence polygon are statistically indistinguishable from the pre-perturbation samples. The method applied here calculates the distance of the sample points to the nearest surface of the 95% confidence polygon and plots these distances against time. The analysis, through the point of data verification and matrix construction, was performed on a microcomputer with software (CAS) developed by Bloom.

The actual stability analysis, which is done in several steps, was accomplished with programs written by Bloom (CAS for Mainframe Computers, EDC, Inc.) in Fortran IV. These programs were run on the IBM computing system at the University of Florida's Northeast Regional Data Center. Computer plotting was performed by a Gould model 5100 electrostatic plotter. Plots produced by the Gould were redrawn for inclusion in this report.

The stability analysis technique as developed by Bloom permits one to define any group of samples as "pre-perturbation" or base-line samples. Since sampling started in late summer, August 1981, and since summer was the period of greatest total density, the pre-perturbation cluster was defined as the months included in the second summer of

sampling (June to October, 1982). This was done to meet the requirement of an adequately described baseline community. This set of months represented the total span of the abundance peak seen during 1982. Thus all individual samples, including those in this artificially created pre-perturbation set, were statistically compared, by means of one-tailed Mann-Whitney U-tests, to this cluster of points. This arrangement of samples permitted me to determine if the late summer samples of 1981 and the last complete summer (1983) in the data set entered the statistically defined cluster of points surrounding the pre-perturbation community. It also created a self-test of the technique with regards to the collection dates included within the pre-perturbation cluster.

A concordance analysis, as described by Grossman et al. (1982) and Moyle and Vondracek (1985), was utilized as a third technique of stability assessment. Statistical procedures for this method, Kendall's coefficient of concordance ($\underline{W}$), are described in Siegel (1956). The months of peak total abundances were compared by this technique to judge year-to-year agreement in the numerical importance of each species.

Results

Seagrass Biomass

Thalassia-blade biomass varied widely during the 12-month period in which it was quantitatively sampled (Figure 2-3). In monthly samples blade biomass peaked in August 1983 and was at a minimum in January 1983. In January visual inspection, by skin-diving, of the study site showed evidence of numerous Thalassia plants but no green blades were apparent.

Population Patterns

During 27 months of sampling, from August 1981 to October 1983, 14 species of shrimp (Table 2-2) were captured in sled hauls taken within the main study area. The caridean species in these samples were subdivided between four families and 12 species. Two penaeid species were also collected in the monthly samples.

The number of occurrences of each species in the series of 27 samples is given in Table 2-3. This table also shows the total numbers and frequencies based on the total number of each species collected during the study. Hippolyte zostericola was the only species which occurred in all 27 samples and it was the numerical dominant in the totaled species counts.

Species richness and the combined abundances of all shrimp species captured in sled samples followed seasonally consistent patterns of fluctuation (Figure 2-4). Fluctuations in species richness were not as regular as changes in

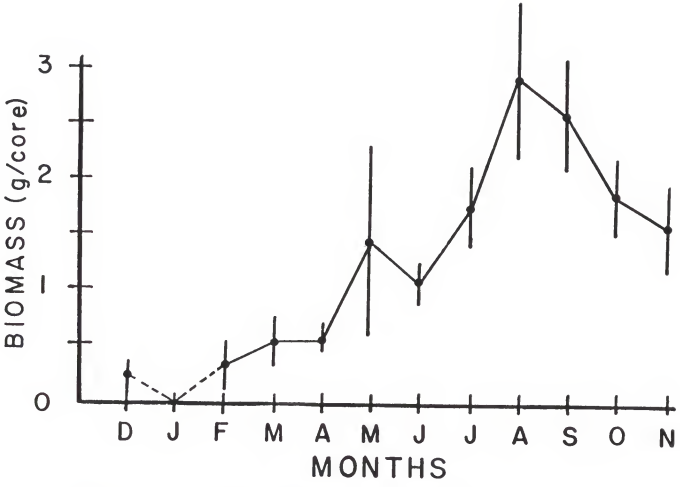


Figure 2-3. Thalassia blade biomass as grams per six inch core. Vertical bars represent ± 1 standard deviation from the mean. Samples were collected from December 1982 through November 1983. The broken line indicates a month of no sampling as explained in the text.

Table 2-2. Shrimp families and species collected at Seahorse Key, Florida during monthly sampling from August, 1981 to October, 1983. Species marked by an asterisk accounted for approximately 97% of all species collected.

Suborder Pleocyemata

HIPPOLYTIDAE

* Hippolyte zostericola (Stimpson)
* Tozeuma carolinense Kingsley
* Thor dobkini Chace
* Latreutes fucorum (Fabricius)
* Latreutes parvulus (Stimpson)

PALAEMONIDAE

* Periclimenes longicaudatus (Stimpson)
* Periclimenes americanus Kingsley
Palaemonetes vulgaris (Say)
Palaemon floridanus Chace

ALPHEIDAE

Alpheus normanii Kingsley

PROCESSIDAE

Processa bermudensis Rankin
Ambidexter symmetricus Manning and Chace

Suborder Dendrobranchiata

PENAEIDAE

Penaeus duorarum Burkenroad
Sicyonia laevigata Stimpson

Table 2-3. A listing of the 14 shrimp species collected at Seahorse Key in order of their total abundances in sled hauls. Frequencies, as percent of all counts, and the number of occurrences of each species in monthly sled collections are also given.

Species	Total Individuals	Percent	Occurrences
Hippolyte zostericola	282706	75.988	27
Periclimenes longicaudatus	38779	10.423	26
Latreutes fucorum	14893	4.003	26
Periclimenes americanus	14553	3.912	22
Tozeuma carolinense	8321	2.237	25
Thor dobkini	4315	1.160	22
Penaeus duorarum	3401	0.914	19
Palaemon floridanus	1780	0.478	7
Palaemonetes vulgaris	1572	0.423	8
Alpheus normanii	1080	0.290	13
Latreutes parvulus	456	0.123	20
Processa bermudensis	129	0.035	7
Sicyonia laevigata	45	0.012	7
Ambidexter symmetricus	10	0.003	3

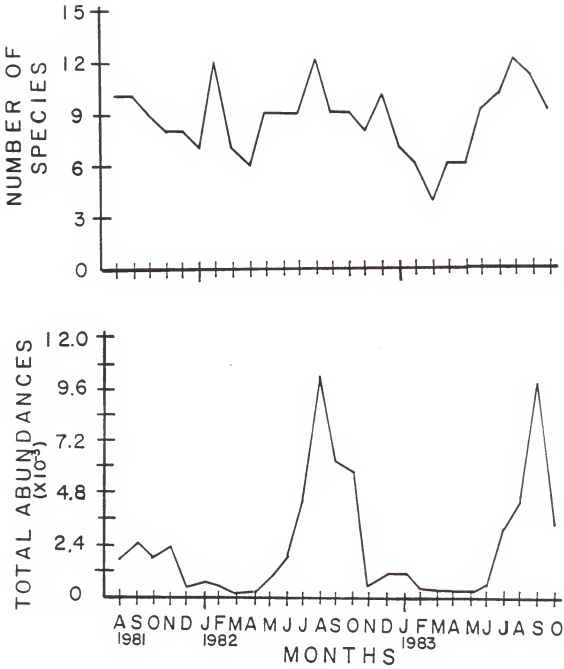


Figure 2-4. a) The total number of species caught on each sampling date from August 1981 through October 1983. b) Total abundance as average shrimp catch per sled haul for all species.

abundance (Figure 2-4). Total numbers of individuals peaked in late summer (August to September) and reached minima during Spring (March to May). Although the seasonal timing of abundance highs and lows were consistent from year to year, there was considerable variability in total numbers of individuals at the annual peaks. Total shrimp abundance was significantly ($P < 0.05$) correlated with average water temperature ($r_s = 0.575$, $N = 27$) and with seagrass biomass ($r_s = 0.615$, $N = 13$). Seagrass biomass was not quantitatively measured on a regular basis prior to December 1982 but the same relationships between blade biomass, temperatures, and total shrimp abundance were apparent throughout the sampling period.

Shrimp densities (Table 2-4) were determined from abundance data as catch per measured sled haul, and from sled efficiency factors. For most species the sled seemed to be an efficient collecting device. Seasonal differences in seagrass biomass could, however, alter the sled's performance. Thus, shrimp counts as the number of individuals per sled haul were used in most analyses.

Hippolyte zostericola was the numerically dominant species collected from this turtle-grass flat. This small hippolytid accounted for 76% of all shrimp collected. Its relative abundance over the study period averaged 81.3% (s.e. = 1.1858) but this figure varied widely from season to season (range = 45.2% to 99.2%). Fluctuations in both relative and absolute abundances over the study period for H. zostericola are illustrated in Figure 2-5. Relative

Table 2-4. Maximum density estimates, average densities, and standard errors of the mean as calculated from sled efficiency factors.

Species	Efficiency Factors	Density		
		Maximum	Mean	S.E.
H. zostericola	1.21	768.721	131.398	19.960
T. carolinense	1.02	25.010	4.497	0.723
Th. dobkini	9.94	235.379	22.755	4.610
L. fucorum	3.63	191.664	28.609	3.862
L. parvulus	8.33	11.995	1.982	0.377
P. longicaudatus	1.00	130.347	20.552	3.743
P. americanus	1.00	113.707	7.766	1.983

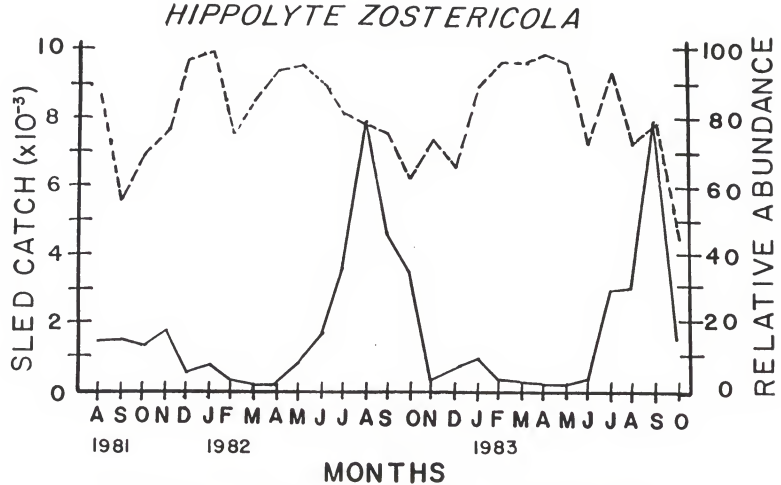


Figure 2-5. Average sled catch (solid line) and relative abundance as percent (broken line) of Hippolyte zostericola at Seahorse Key from August 1981 through October 1983.

abundances (Figure 2-5) for H. zostericola exceeded 95% during the winter months of each complete sampling year. Yearly peaks in absolute abundance occurred in the late summer and fall (Nov., 1981; Aug., 1982; and Sep., 1983). On these sampling dates, the yearly peaks of shrimp abundances, H. zostericola accounted for 76.5, 77.2, and 77.4%, respectively, of the total shrimp abundance. Hippolyte was the only species present in all 27 sets of samples and it outnumbered all other species in all but one of these samples (October 1983, when Periclimenes longicaudatus was numerically dominant).

Periclimenes longicaudatus was the second most common species captured during the study period. Absolute and relative abundances for this species during the sampling period are illustrated in Figure 2-6. Over 27 months of sampling its mean relative abundance was 6.8% (s.e. = 0.9192, range = 0% to 51.1%). Numbers of individuals of P. longicaudatus collected in sled hauls peaked each year from September to October. Before and after these sudden population explosions P. longicaudatus virtually disappeared from the grassflat. It was collected in all but one set of monthly samples but most often it was present in very low abundances.

Latreutes fucorum was ranked third in total abundance among shrimps at Seahorse Key. Peaks in absolute and relative abundances for L. fucorum are given in Figure 2-7. The average relative abundance for this species was 4.6% (s.e. = 0.4389, range = 0% to 15.7%). Peaks of absolute abundance

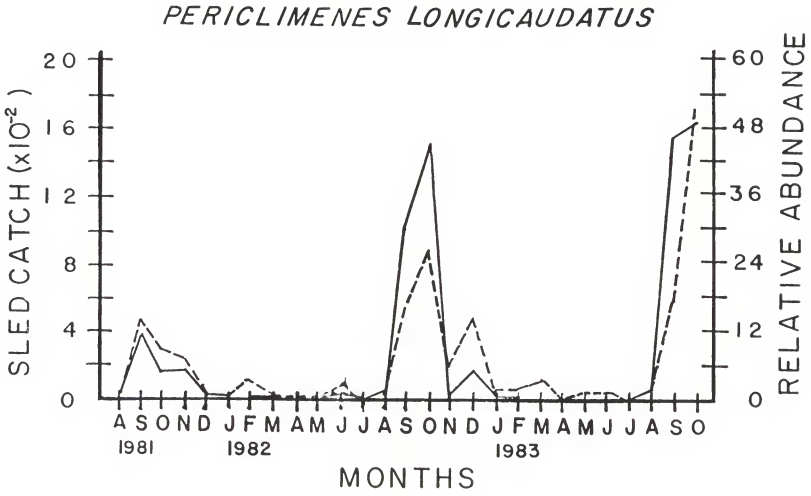


Figure 2-6. Average sled catch (solid line) and relative abundance as percent (broken line) of Periclimenes longicaudatus at Seahorse Key from August 1981 through October 1983.

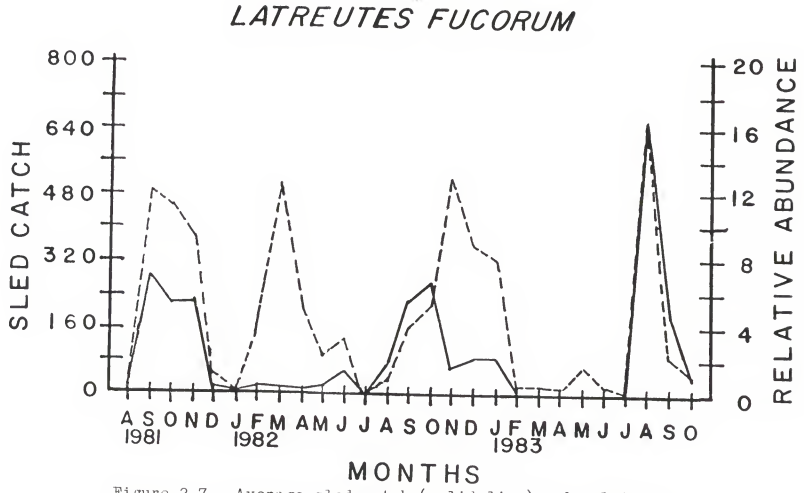


Figure 2-7. Average sled catch (solid line) and relative abundance as percent (broken line) of Latreutes fucorum at Seahorse Key from August 1981 through October 1983.

for this species occurred during late summer to early fall. During 1981 and 1982 the yearly maxima are of similar magnitude. The 1983 peak, occurring in August, was substantially higher than the population highs of the previous two years. Latreutes fucorum, like P. longicaudatus, was found in all but one set of monthly samples.

The fourth most abundant shrimp species at Seahorse Key was Periclimenes americanus. The absolute abundance of P. americanus was very low (Figure 2-8) throughout most of the study period. Its mean relative abundance was 1.6% (s.e. = .2706, range = 0% to 14.2%). It was usually present (22 of 27 samples) but was seldom numerous. Seasonal peak abundances for P. americanus occurred in August 1982 and September 1983. No seasonal peak was apparent in the 1981 samples. This lack of an increase in numbers could have been due to an increase and decline which occurred before sampling began.

Tozeuma carolinense, the fifth ranked species among carideans and penaeids at Seahorse Key, accounted for an average relative abundance of 3.2% (s.e. = .4604, range = 0 to 20.5%). Increased numbers of individuals were present in late summer to early fall (Figure 2-9). Tozeuma carolinense was collected during all but two months of the study period. In this shallow-water Thalassia bed Tozeuma was common but never abundant.

Thor dobkini ranked sixth among shrimps caught at Seahorse Key. Peaks in the average number of individuals in sled haul replicate samples occurred in late summer (August

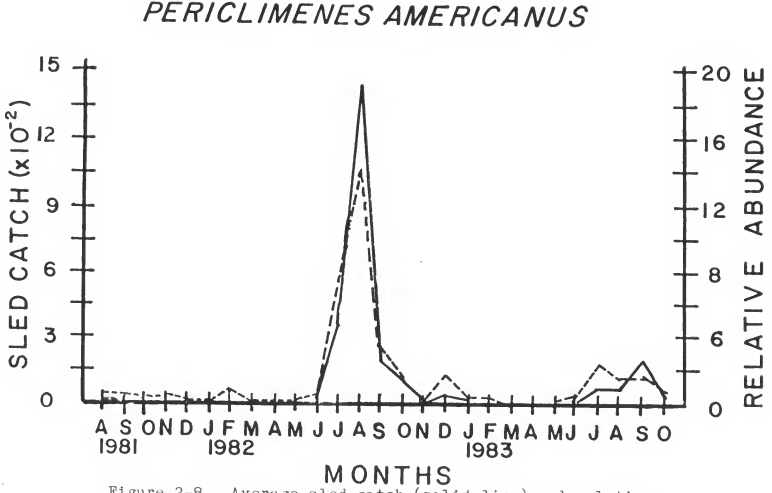


Figure 2-8. Average sled catch (solid line) and relative abundance as percent (broken line) of Periclimenes americanus at Seahorse Key from August 1981 through October 1983.

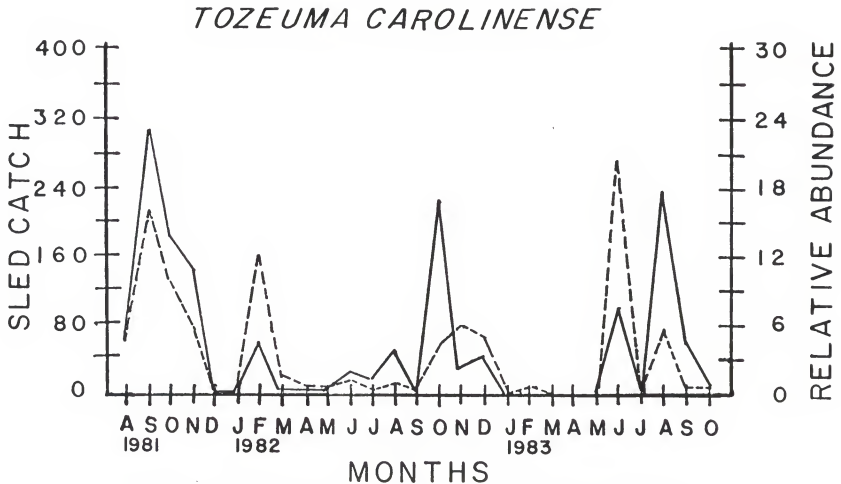


Figure 2-9. Average sled catch (solid line) and relative abundance as percent (dashed line) of Tozeuma carolinense at Seahorse Key from August 1981 through October 1983.

1982 and 1983) to early fall (September 1981) (Figure 2-10). The mean relative abundance of Thor during the study period was 0.8% (s.e. = 0.1054, range = 0 to 4.2%). The 1982 peak abundance was much higher than in either 1981 or 1983. Thor occurred in 22 of the 27 sets of monthly sled haul samples.

Latreutes parvulus was ranked eleventh among the 14 shrimps caught at Seahorse Key. Absolute abundances of this shrimp (Figure 2-11) peaked with much less regularity than those of the other species considered up to this point. In 1981 peak abundances for L. parvulus occurred in November, in 1982 peak numbers per sled haul were reached in both July and September, and in 1983 the annual peak occurred in July. Other abundance peaks may have occurred in 1981 and 1983 before and after the sampling study. L. parvulus was present in 20 of the 27 sample sets collected at Seahorse Key. Relative abundances ranged from 0 to 3.6% (mean = 0.314%, s.e. = 0.0766).

The seven species considered so far are those which were obviously most similar in size and which were originally thought to be similar in diet. They also accounted for over 96% of all shrimp collected at Seahorse Key. The other species collected at Seahorse Key were either larger, trophically distinct (as documented by Leber, 1983), nocturnally active (diurnal burrowers) (Greening and Livingston, 1982), and/or much more seasonally present. Table 2-3 gives the total numbers of these species caught over the 27 months of collecting, the number of occurrences of each species in

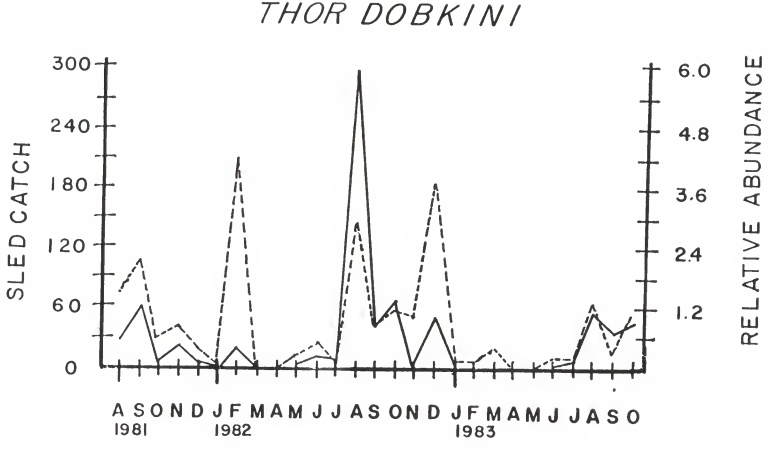


Figure 2-10. Average sled catch (solid line) and relative abundance as percent (broken line) of Thor dobkini at Seahorse Key from August 1981 through October 1983.

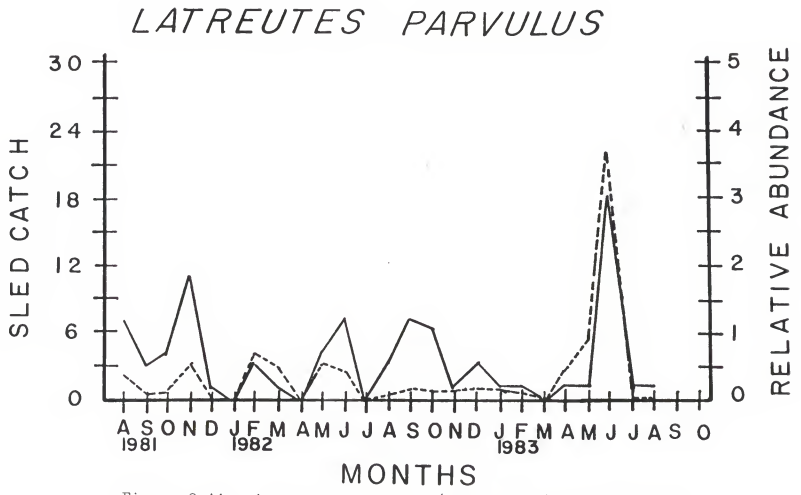


Figure 2-11. Average sled catch (solid line) and relative abundance as percent (broken line) of L. parvulus at Seahorse Key from August 1981 through October 1983.

the samples, and their frequencies based on the total number of shrimps collected during the study.

Spearman rank correlation analyses of caridean abundances (Table 2-5) demonstrated that in almost all cases correlations between species pairs were positive at statistically significant levels. The only exceptions, which were positive but not significant correlations, involved Latreutes parvulus. The high percentage of significant positive correlations suggests that populations of these species are affected similarly by various environmental factors. A rank correlation analysis of individual species counts against water temperature, salinity, and seagrass biomass (Table 2-6) demonstrated that abundances of five of the seven species were positively and significantly correlated to water temperature and/or seagrass biomass. Abundances of L. parvulus were not significantly related to either of these two factors. This analysis indicated that L. parvulus populations may have been influenced by salinity fluctuations. Periclimenes longicaudatus showed a lack of significant correlation to any of these environmental factors. Instead, sudden increases in its abundance, irrespective of seagrass biomass and temperature, occurred at regular yearly intervals (Figure 2-6).

Table 2-7 lists the occurrence of seasonal peaks for each of the seven caridean species. The table shows, in most cases, that the peak levels of monthly abundance of Hippolyte zostericola usually precede or follow the seasonal peaks of the other four hippolytid species. Abundance peaks

Table 2-5. Correlation matrix of the dominant caridean shrimp abundance patterns from August 1981 to October 1983 at Seahorse Key, Florida. The lower hemimatrix gives values of Spearman's rho while the upper hemimatrix indicates the significance of each matching value. In the upper hemimatrix asterisks represent statistically significant correlation (* $P \leq 0.05$, ** $P \leq 0.01$) and N.S. indicates a non-significant correlation ($P > 0.05$).

	H.p.	T.c.	Th.d.	L.f.	L.p.	P.a.	P.l.
H.p.	1	**	**	**	n.s.	**	**
T.c.	.5667	1	**	**	**	**	**
Th.d	.7883	.7611	1	**	*	**	**
L.f.	.5401	.6444	.7028	1	*	**	**
L.p.	.2622	.5408	.3690	.4021	1	n.s.	n.s.
P.a.	.9231	.5787	.8298	.4653	.2710	1	*
P.l.	.6052	.6226	.7873	.7868	.2295	.5984	1

Table 2-6. Spearman rank correlation coefficients of caridean abundances with mean seawater temperature, mean salinity and seagrass biomass as above-ground plant biomass. The significance of the correlation coefficients are indicated with asterisks (* $P \leq 0.05$, ** $P \leq 0.01$).

Species	Water Temperature[a]	Salinity[a]	Seagrass Biomass[b]
H. zostericola	+0.5709*	+0.0306	+0.6909*
T. carolinense	+0.4855**	+0.3729*	+0.6606*
Th. dobkini	+0.4460*	+0.1487	+0.7032*
L. fucorum	+0.1779	+0.3220	+0.8545**
L. parvulus	+0.2965	+0.3857*	+0.1012
P. americanus	+0.6043**	-0.0656	+0.625*
P. longicaudatus	+0.0763	+0.1064	+0.3918

a N = 27, August 1981 to October 1983.
b N = 11, December 1982 to October 1983.

Table 2-7. Months of peak abundances for the dominant group of caridean shrimps found at Seahorse Key, Florida.

Species	Years		
	1981	1982	1983
Hippolyte zostericola	Aug, Nov	Aug	Sep
Periclimenes longicaudatus	Sep	Oct	Sep
Latreutes fucorum	Sep	Oct	Aug
Periclimenes americanus	Aug	Aug	Sep
Tozeuma carolinense	Sep	Oct	Aug
Thor dobkini	Sep	Aug	Aug
Latreutes parvulus	Nov	Jun, Sep	Jun

of the two palaemonids frequently coincided with those of H. zostericola. The separation of peaks, as described, among the hippolytids may have resulted from density-dependent interactions.

Body Size

Table 2-8 presents the size ranges and mean sizes of both the overall population and of brooding females for each of the seven carideans considered in this study. Tozeuma carolinense was by far the largest species of this selected group. The remaining species were very similar in size.

Except for the two largest species, Tozeuma carolinense and Periclimenes longicaudatus, sizes at recruitment (the smallest shrimp recorded for each species) and sizes at female sexual maturity (the smallest brooding female of each species), were quite similar (Table 2-8). The recruits and smallest brooding females of T. carolinense and P. longicaudatus were separated from the other species and from each other with respect to size.

Size ratios of sequentially arranged pairs of larger to smaller shrimps are given for the overall populations (juveniles, males, and all females) and for embryo-carrying females. Four of the species pairs had mean body size ratios for all individuals and for brooding females of less than the predicted ratio of 1.28. Only the pairs of Latreutes fucorum and Periclimenes longicaudatus and of P. longicaudatus and Tozeuma carolinense exceeded Hutchinson's ratio.

Table 2-8. Sizes of shrimps at main study site. Measurements of total length in millimeters are presented for brooding females and entire populations over the 27 months of sampling. Hutchinson's ratios of larger to smaller species are also given for sequential pairs in a hierarchy of increasing size.

Species	Size range length (in mm) overall	females	Size (mean ±SD) overall	females	Hutchinson's ratio overall	females
L. p.	2.6- 8.9	4.9- 8.9	4.5 ±1.04	6.3 ±0.62	1.12	1.19
T. d.	2.0-10.9	6.4-10.9	5.0 ±1.31	7.5 ±0.91	1.09	1.07
H. z.	2.0-10.4	5.3-10.4	5.5 ±1.61	8.0 ±0.97	1.04	1.08
P. a.	2.9-12.1	5.6-11.8	5.7 ±1.53	9.0 ±0.70	1.03	1.04 (Lf)
L. f.	2.4-11.8	6.8-12.1	5.9 ±1.60	8.7 ±1.25	1.48	1.36 (Pa)
P. l.	4.0-15.9	9.4-15.1	8.6 ±1.99	12.3 ±1.54	1.75	1.74
T. c.	4.2-27.3	14.4-26.0	15.1 ±3.87	21.4 ±1.73		

Size-Frequency Distributions

Changes in the size distributions through time of four of the five most abundant species are illustrated in Figure 2-12. Periclimenes americanus, the fourth-ranked species, was not included in this set of histograms due to its usually low abundances in samples throughout most of the sampling period.

Hippolyte zostericola, the numerically dominant species, showed (Figure 2-12a) no obvious changes in size structure throughout the sampling period. Its size frequency distributions were bimodal or polymodal from August 1981 through October 1983. Recruits apparently entered the population throughout the year. Adults were also continuously present.

Latreutes fucorum's pattern of change (Figure 2-12b) in size distributions was similar to that shown by Hippolyte zostericola. Small and large individuals were present throughout the yearly cycles of population flux. Latreutes fucorum was less abundant than Hippolyte zostericola but individuals of this species were present in 26 of the 27 samples. As was true of H. zostericola its size-frequency distribution curves were usually bimodal or polymodal in overall form.

Changes in the size-frequency distribution patterns of Tozeuma carolinense (Figure 2-12c) were very irregular. Tozeuma carolinense was present in 25 samples but never in great abundances. This species was found in greatest numbers in beds of the round-bladed seagrass, Syringodium

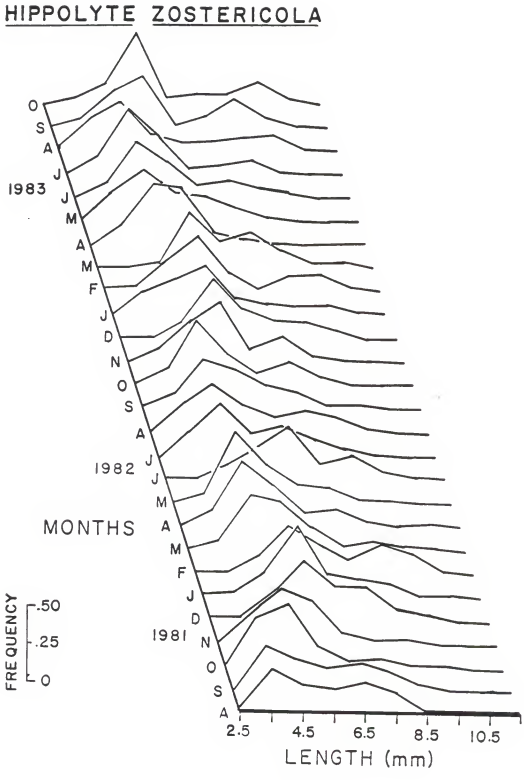


Figure 2-12 a-d. Size frequency distributions in monthly samples for the four most abundant shrimps collected at Seahorse Key. a, Hippolyte zostericola.

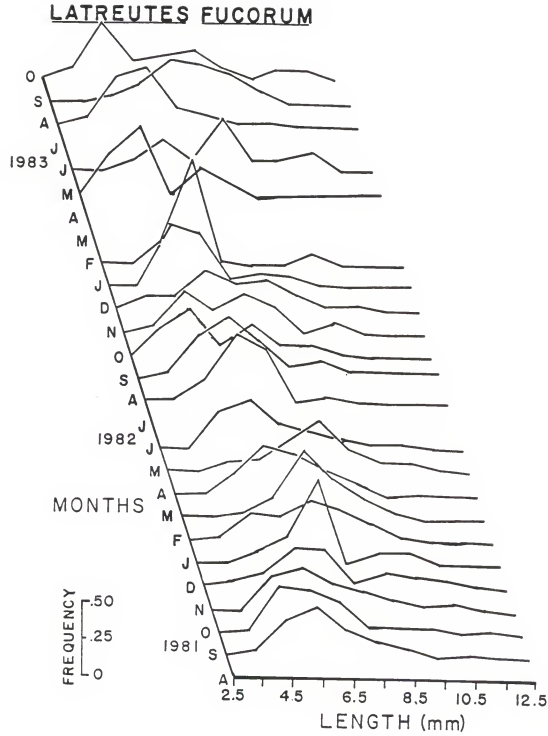


Figure 2-12--continued. b, Latreutes fucorum.

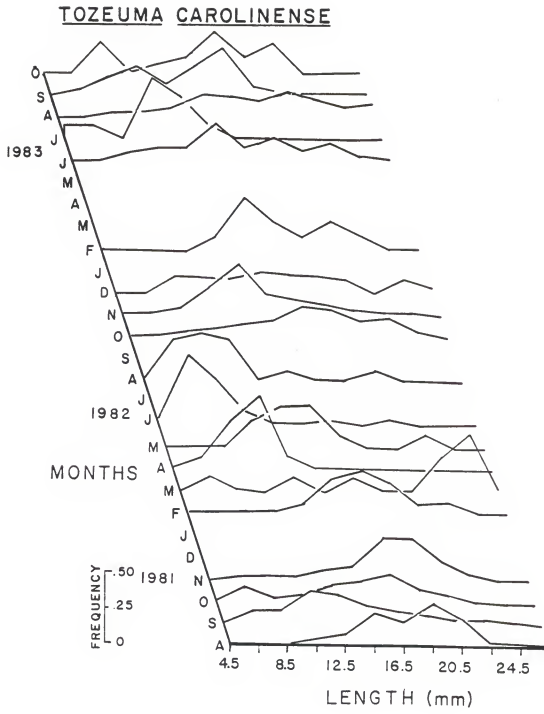


Figure 2-12--continued. c, Tozeuma carolinense.

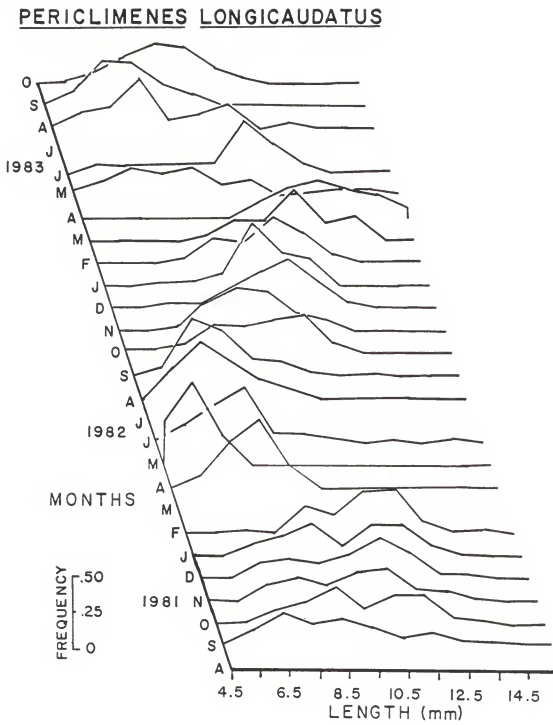


Figure 2-12--continued. d, Periclimenes longicaudatus.

filiforme. Thus T. carolinense may have been present in the main study site, an almost monospecific bed of short-bladed Thalassia, as transients or occassional stragglers.

Periclimenes longicaudatus, the second most abundant species, displayed (Figure 2-12d) a distinctly different, unimodal size-frequency distribution pattern throughout most of the sampling period. Periclimenes longicaudatus was present in all but one sample (Table 2-3), but it was generally present in low abundances throughout most of the year. After the fall increases (Figure 2-6) of 1981 and 1982, abundances of this species dropped precipitously. During most of the year the population consisted entirely of larger individuals which probably belonged to a single cohort because little or no recruitment occurred after the early fall months. This was especially evident in the population cycle which began in August 1982 and ended in April 1983. The same trend can be seen in samples taken from September 1981 to February 1982.

Recruitment and Brooding

Annual cycles in the densities of females with broods are shown in Figure 2-13. Hippolyte zostericola was the only species which had brooding females present throughout the entire sampling period. Densities of females carrying broods peaked for most species during late summer to early fall. Latreutes parvulus was the only species that did not follow this general pattern.

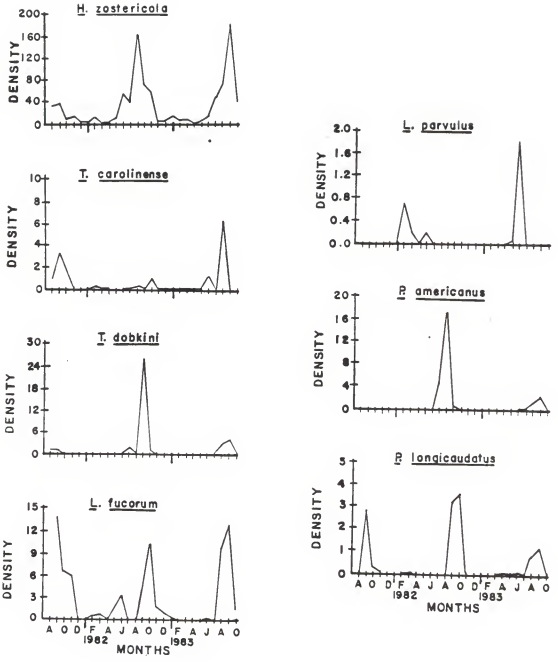


Figure 2-13. Densities (numbers/m^2) of females with broods from August 1981 through October 1983.

Latreutes parvulus berried females were present from February through May of 1982 and during May and July of 1983. These peaks of reproductive activity were clearly offset from those observed for the other six species. Very few brood-carrying females of L. parvulus were collected.

Although reproductive activity, as indicated by the presence of brooding females, usually peaked during late summer and early fall months, much smaller peaks were observed for some species during early winter. These secondary winter increases in reproduction are evident in Figure 2-13 for Hippolyte zostericola (1981, 1982, and 1983), Tozeuma carolinense (1982), and Latreutes fucorum (1981, 1982, and 1983). Thor dobkini did not produce broods during the two winters included in the sample set.

Peaks of recruitment (Figure 2-14) usually coincided with increased numbers of brooding females and with population peaks in general. In a few cases recruitment peaks preceeded increases in densities of brood-carrying females by several months. This was especially obvious in the case of Latreutes parvulus when recruitment peaked in November 1981. Brooding females, presumably from this cohort, first appeared three months later during February 1982. A second, smaller increase in brooding female densities occurred during May 1982. These individuals may have been members of the November cohort which survived to produce a second brood.

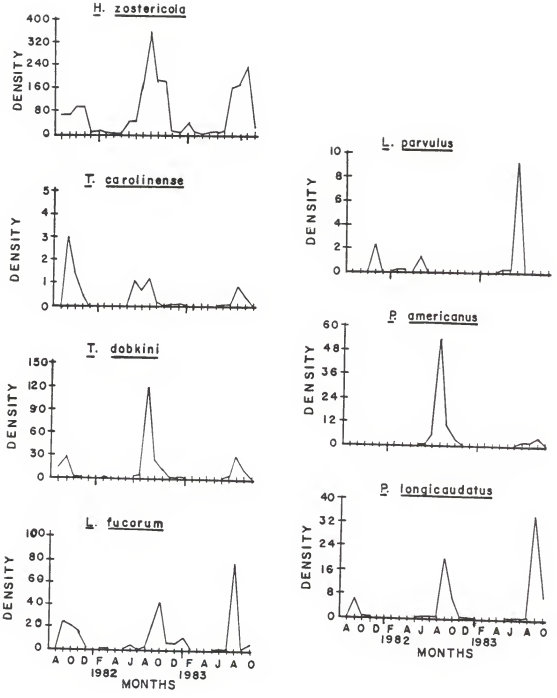


Figure 2-14. Densities (numbers/m^2) of juvenile shrimps from August 1981 through October 1983

Distribution Across Seagrass Zones

Relative abundances of each of the 14 shrimp species present in the intertidal grassbeds of Seahorse Key varied from zone to zone (Figure 2-15). Hippolyte zostericola was the most numerous shrimp in each of the parallel seagrass beds. In the Halodule zone Penaeus duorarum juveniles ranked second in abundance. Several species, including Tozeuma carolinense, Thor dobkini, Latreutes parvulus, and Latreutes fucorum, were not found in the Halodule zone.

In the seaward-most zone, the Syringodium bed, Hippolyte zostericola and Tozeuma carolinense were present in almost equal abundances. All five of the other selected shrimps were also found in this zone. In the bed of short-bladed Thalassia, the primary study site, Periclimenes longicaudatus was, on this date, second in abundance to H. zostericola. As evidenced from the results of the monthly sampling program the abundances of all species, in this zone, varied greatly throughout the sampling program. The relative and total abundances of each species in the Halodule and Syringodium zones undoubtably also varies greatly from month to month.

Size-frequency distributions for H. zostericola, P. longicaudatus, and L. fucorum, collected on this same date (September, 1983) were compared across these three zones. This was done to determine if species segregated by size classes across the three microhabitat types. Minor differences in size distributions among species were seen but there were no obvious zones of recruitment.

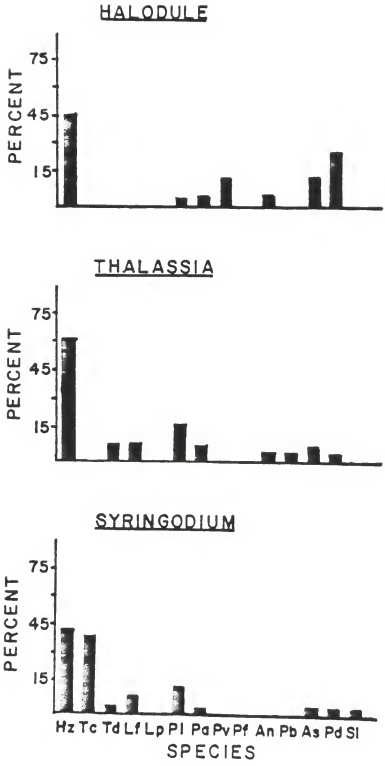


Figure 2-15. Relative abundances, during September 1983, of shrimps in each of the three grassbed zones at Seahorse Key. Latreutes parvulus was not collected on this date.

Community Patterns

Fluctuations in species numbers were somewhat less regular than the yearly patterns of total shrimp abundance (Figure 2-4). Species numbers always peaked during late summer (August 1981, 1982, and 1983) but were also high during both February and December of 1982. Diversity (H') and relative eveness patterns (Figure 2-16) peaked twice each sampling year but otherwise demonstrated little evidence of a definite seasonal pattern. Diversity also varied greatly from year to year at the seasonal peaks of shrimp abundance.

Classification Analyses

Dendrograms produced by the techniques described in the methods section are shown in Figures 2-17 and 2-18. Four clusters were evident in the first dendrogram (Figure 2-17), produced from log (base 10) transformed data. Two of the clusters, A and C, showed definite evidence of seasonality. Cluster A is composed almost entirely of late summer and fall samples from all three years of the study period. Cluster A contains all of the September and October samples. Cluster C is composed of only summer months (July and August). The various years of the sampling period are also represented in this cluster which indicates the presence of repeatable seasonality over the length of the sampling period. No groupings appear to be based on within-year similarities.

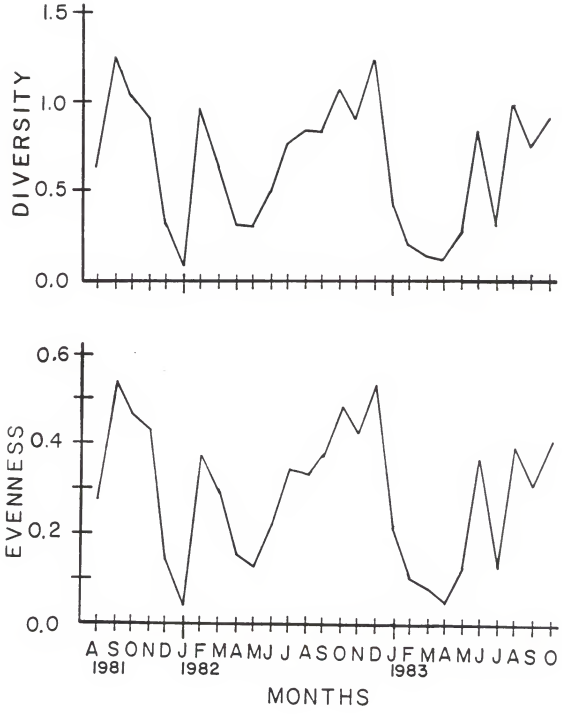


Figure 2-16. Diversity (H') and evenness of the shrimp assemblage collected at Seahorse Key from August 1981 through October 1983.

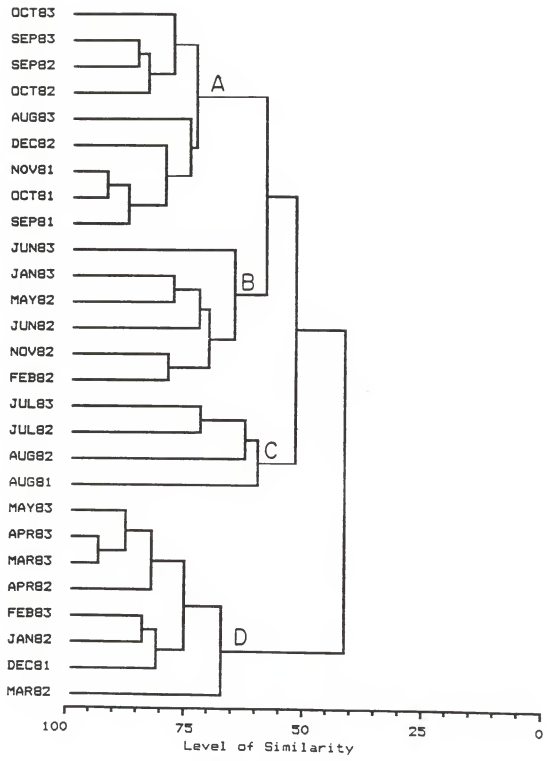


Figure 2-17. Dendrogram produced from log-transformed data using Czekanowski's Quantitative Index with a group-average sorting strategy.

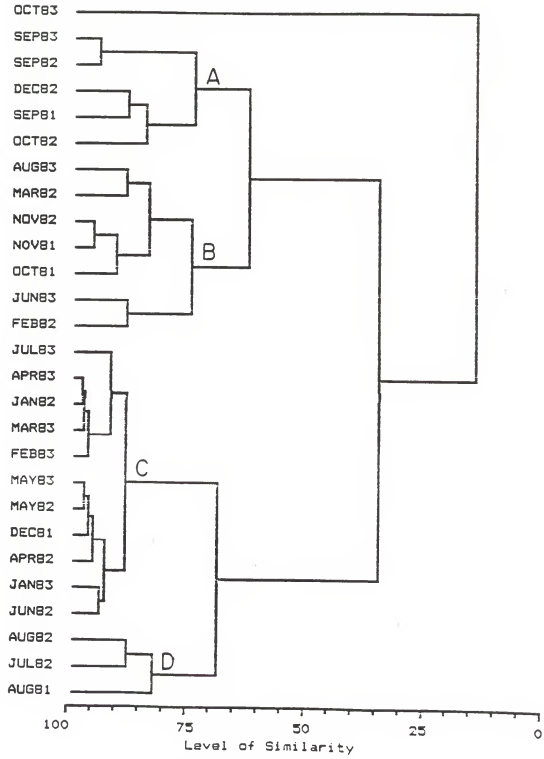


Figure 2-18. Dendrogram produced from frequency transformed data using Czekanowski's Quantitative Index with a flexible sorting strategy.

Samples included in clusters B and D were not seasonally coherent. Cluster B was composed of winter, spring, summer, and fall samples. Cluster D included 5 spring samples but also included 3 winter samples. As was the case for clusters A and C, clusters B and D did not show evidence of being based on patterns of within-year similarities. The months included in these two clusters represented periods when shrimp abundances (Figure 2-4), temperatures (Figure 2-2), and seagrass densities were low (Figure 2-3).

A dendrogram produced from frequency transformed data with group average sorting produced a high degree of chaining between months. For this reason the second dendrogram shown here (Figure 2-18) was produced from frequency transformed data but with a flexible sorting strategy (beta = -0.25). Four main clusters were also evident in this second dendrogram. A single month, October 1983, was set apart from the four larger clusters as an outlier. This month was unique among the 27 sets of monthly samples in that P. longicaudatus outnumbered the otherwise numerically dominant H. zostericola. Cluster A contained all three September samples and samples collected during October and December of 1982. Cluster D was the only other cluster in this dendrogram which appeared to be more or less seasonally coherent. Cluster D contained only summer samples but other summer samples were contained in clusters B and C. Spring samples which were found together in the $\log_{10}$ transformed dendrogram were more scattered in the frequency transformed dendrogram. In both dendrograms fall and late summer samples

fell out in two distinct clusters. No distinct patterns were evident among the spring and winter months in either dendrogram. These months included periods when the various shrimp populations were declining in late autumn, were at their winter low densities, or were beginning to increase in the early spring. Thus both dendrograms, though produced by different techniques, offer evidence of a repeating community pattern occuring between years within this caridean dominated shrimp community.

Community Concordance

Kendall's test of rank concordance was utilized to judge the year-to-year agreement in the numerical importance of species. This test did not use the entire data set in that it included only the three months when abundances reached their yearly peaks. It did allow consideration of the month of peak abundance included in the base-line community samples of the Bloom method of stability assessment. The results (Table 2-9) indicated a statistically significant level of concordance at peak abundance levels between years for this caridean dominated community.

Stability Analysis

Shrimp abundances reached peak levels during the late summer to early fall of each year included in the 27 months of samples. As shown in Figure 2-4 shrimp densities declined in late autumn and were quite low during the winter and spring months. Thus the sampling period spans two complete cycles of defaunation and recovery.

Table 2-9. Average sled haul abundances of shrimps at Seahorse Key during the observed annual peaks in total abundance. The probability value is that generated by Kendall's *W* and it indicates the chi-square derived probability that the abundance ranks of the shrimps are not correlated during the three months of peak abundances. Species indicated by asterisks were not used to calculate Kendall's *W*.

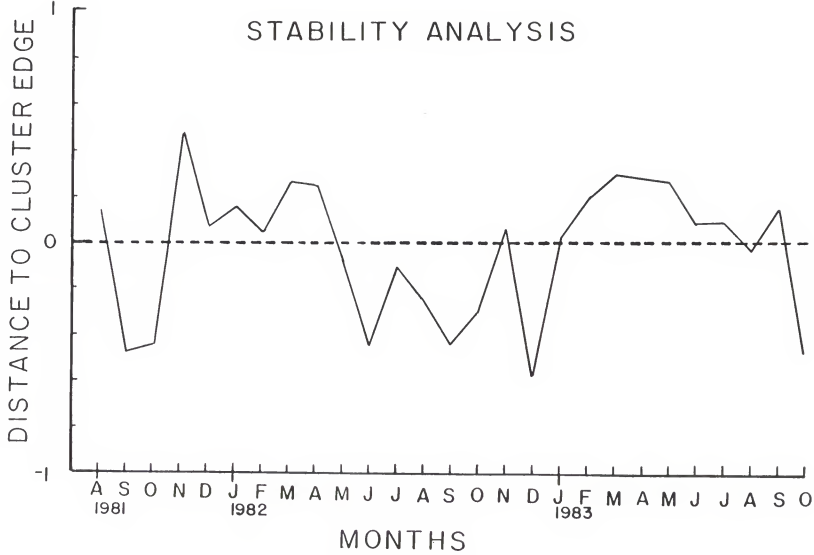
Species	November 1981	August 1982	September 1983
H. zostericola	1763.2	7941.3	7817.3
T. carolinense	141.8	50.7	60.0
P. longicaudatus	174.5	42.7	1542.7
L. fucorum	230.8	82.7	202.3
Th. dobkini	20.8	296.0	34.7
L. parvulus	10.8	2.7	0.0
P. americanus	6.3	1421.3	178.7
Pen. duorarum	0.0	224.0	24.0
Pa. floridanus	0.0	29.3	54.7
P. vulgaris	0.0	48.0	8.0
S. laevigata	2.0	0.0	2.7
*Am. symmetricus**	0.0	0.0	0.0
*Pr. bermudensis**	0.0	5.3	0.0
*Al. normanii**	0.0	69.3	5.3

$W = 0.679$, $P < 0.010$

The results of the Bloom technique of stability analysis on a quantitative data set, as described in the methods section, are illustrated in Figure 2-19. The edge of the 95% confidence limit envelope corresponds to the 0-line of this figure. As stated in Santos and Bloom (1980) once a point falls below this line it is statistically indistinguishable from the pre-perturbation points. The pattern produced by defining the pre-perturbation points as the summer and early fall months of 1982 showed that the community did recover the following year. Resilience was also indicated in 1981, following a presumably similar annual cycle of defaunation and repopulation, and in 1983, when points fell below the edge of the confidence limit envelope.

The points most distant from the envelope edge were not seasonally consistent from year to year. In 1981 month 4 (November) and in 1983, month 20 (March) were most distant from the statistically defined envelope's edge. On three occasions single points fell below the edge of the recovery envelope. In December 1982, the position of the point may have resulted from an increase in the number of species (Figure 2-4) and a small rise in the total sled catch (Figure 2-4). The position of the August 1983 point, also below the recovery line, coincides with a peak in diversity (Fig 2-16). Diversity decreased in September 1983, but increased again in October. These fluctuations in diversity were mirrored by changes in the distance to the cluster edge for each of these two months.

Figure 2-19. Results of the "Bloom technique" (Santos and Bloom, 1980) of stability assessment. Data were log-transformed prior to the analysis.


STABILITY ANALYSIS
DISTANCE TO CLUSTER EDGE
1
0
-1
A S O N D J F M A M J J A S O N D J F M A M J J A S O
1981
1982
1983
MONTHS

Discussion

Assemblage Characteristics

In comparison to the caridean fauna of other seagrass beds the shrimp densities observed at Seahorse Key were quite high (Table 2-10). In two of the cases reported in this table a large mesh size may have lowered the catch efficiency of the sampling devices. Bauer (1985), however, used a small mesh size and reported that his pushnet collected efficiently at his Thalassia-bed study site. The densities he reported were still an order of magnitude lower than those observed at Seahorse Key. A reviewer of Bauer's paper suggested that the shallowness of his collecting site may have protected its caridean fauna from predatory fishes. Bauer rejected this reasoning but it seems to be a likely explanation for the super-abundance of carideans observed at Seahorse Key.

Carr and Adams (1973) and Reid (1954) identified numerous fish species which feed on small shrimps in northern Gulf of Mexico seagrass habitats. Although not formally observed during this study the seaward Syringodium zone seemed to have more fishes at higher densities than was true of the primary study site. Most low tides left the study site grassbed shallowly covered. On the lowest spring tides the entire grassbed was exposed. During these periods shrimps were present beneath mats of Thalassia and algae or in numerous small tidal pools. Most of the fishes, with the exception of gobies and pipefishes, moved to deeper water.

Table 2-10. Densities (numbers/m^2) and number of species of caridean shrimps from seagrass beds in various localities. Methods of collection and mesh sizes of the nets used in the collecting devices are also listed.

Sources	Location	Average Density	Number of Species	Sampling Device	Mesh Size
Brook (1975)	Card Sound, Florida	28.2	--	Suction Dredge	3.0
Gore (1981)	Indian River, Florida	74.1	16	Drop net	3.2
Howard (1984)	Western Port, Australlia	66.3	4	Beam trawl	1.0
Bauer (1985)	Dorado, Puerto Rico	49.0	16	Push net	1.0
Marshall	Seahorse Key Florida	217.6	14	Epibenthic sled	1.2

Thus the caridean fauna may have been partially protected from predators by low tides.

Epiphyte diversity may have been an important factor contributing to the high shrimp densities observed at Seahorse Key. Results of dietary comparisons among the smaller shrimps (Chapter III) indicated that the hippolytids are micrograzers which feed heavily on epiphytic algae. Thursby (1976) reported 91 species of algal epiphytes from seagrass beds in this same area. Species richnesses of algae epiphytes on seagrass blades, from other areas, are generally lower (Virnstein et al., 1984) than reported by Thursby.

Seagrass biomass had a strong influence on the total abundance of the shrimp assemblage and it may have also contributed to the density differences seen between the sites listed in Table 2-10. In general Thalassia biomass (g dry wt/m^2) is higher on the west coast of Florida than in Puerto Rico or on Florida's east coast (Zieman, 1982). Thalassia biomass, however, seemed quite low at the study site in comparison to the nearby deeper seagrass beds. Unfortunately, each of the studies listed in Table 2-10 used different measures of plant biomass (whole plant, aboveground plant biomass, etc.) and/or blade counts making site-specific comparisons impossible.

An additional factor contributing to the observed density levels may have been the efficient operation of the epibenthic sled. Howard (1981), the only other author to report species-specific efficiencies for a collecting device, found that the efficiency of his beam-trawl ranged

from 1.2, for Macrobrachium intermedius (a relatively large palaemonid) to 39.2 for Hippolyte caradina (a small hippolytid). My epibenthic sled was more efficient at collecting small species (Table 2-4) but was less efficient at collecting larger shrimps. Presumably the sled's cutting blade and weight produced its high catch efficency for hippolytids and palaemonids. During daylight hours the sled did not adequately sample the deep-burrowing species (Alpheus normanii, Processa bermudensis, and Ambidexter symmetricus).

The size of individual populations and the total abundance of shrimps at Seahorse Key fluctuated in regular annual cycles with water temperature and seagrass aboveground biomass. The community measures of species richness, diversity, and eveness, however, followed patterns that were seasonally consistent over the sampling program. Seagrass biomass, as an index of habitat complexity, has been widely reported (as reviewed in Chapter I) to have a major role in regulating the abundances of small crustaceans. Temperature, in turn, influences seagrass growth patterns (Zieman, 1982) and regulates crustacean growth rates and reproductive cycles (Alon and Stancyk, 1982). Summer high and winter low temperatures may have, on occasion, caused shrimp mortalities in the shallow Seahorse Key grassbeds. Temperature and salinity tolerances, however, are unknown for any of the carideans considered in this study. Hippolyte zostericola seemed to have the broadest tolerances since it was continuously present in these seagrass beds. Brooding and recruitment were also observed for this species throughout

the sampling period. Similarly, Latreutes fucorum was collected in most samples and brooding females were present on the majority of collecting dates. In general, peaks in brood production and recruitment occurred during the warmer months and coincided with population peaks. Latreutes parvulus was the only species with winter-time peak levels of reproduction and recruitment.

Size-frequency distributions of Hippolyte zostericola, Tozeuma carolinense, Latreutes fucorum, and Periclimenes longicaudatus showed three distinct patterns through time. The two hippolytids, H. zostericola and L. fucorum, had similar bimodal to polymodal size frequency distributions throughout the sampling period. T. carolinense, which seemed to be an accidental resident of the shallow-Thalassia bed displayed irregular changes in its monthly size-frequency distributions. No distinct peaks of recruitment were observed. P. longicaudatus recruitment occurred most heavily in early fall. During the remainder of the year (especially apparent from September 1982 through April 1983) a single cohort was present. This cohort gradually increased in size and completely disappeared in spring.

Abundance histograms and size-frequency distributions across the grassbed zones, constructed from collections made during September 1983, indicated that certain species had preferred zones of residence and recruitment. Hippolyte zostericola was the most broadly distributed species. It occurred in substantial numbers in all three grassbeds and it showed no major differences in size-frequency distibution

between these zones. Juvenile Penaeus duorarum, Ambidexter symmetricus, and Palaemonetes vulgaris were found at moderate densities in the Halodule bed but no other shrimps were abundant in this zone.

Tozeuma carolinense was nearly equal in abundance to Hippolyte zostericola in the Syringodium bed but was not significantly present in the Thalassia zone. Tozeuma carolinense's affinity for the round blades of Syringodium is mentioned by Ewald (1969). Most of the other species were present in the Thalassia and Syringodium beds. Size frequency distributions of Latreutes fucorum and Periclimenes longicaudatus indicated that they recruited to both of these grassbed types. Presumably this was true of the other hippolytids and Periclimenes americanus but insufficient numbers of these species on this collection date prevented me from constructing the size-frequency histograms necessary to demonstrate this point.

Body-size ratios among the four small hippolytids (for the entire populations and for brood-carrying females) and Periclimenes americanus (the overall population) were less than the value of 1.28 predicted by Hutchinson (1959). The overlapping and small sizes of these grassbed shrimps may reflect their common use of microalgae as foods. Their diminuitive sizes may also reflect a common need to utilize crevices among seagrass blades as refuges from predatory fishes and crustaceans. Hines (1982) suggested this conclusion in regard to body size overlap in an assemblage of spider crabs. The species, Tozeuma carolinense and

Periclimenes longicaudatus, with ratios exceeding 1.28 in this series, were dissimilar from the smaller set of species in other potentially ecologically important ways. The body of P. longicaudatus, an active predator (Chapter III), is unique in that it is completely transparent. Thus refuge among seagrass blades may not be as important to this species. T. carolinense, as mentioned, was most abundant in Syringodium beds. Its morphology and presumably its concealment strategies are determined by its association with Syringodium (Ewald, 1969; Vann, 1980; personal observation).

Despite numerous differences in the each of the factors discussed to this point, most of the species in this assemblage of carideans responded similarly, as evidenced by correlation anlyses, to temperature and seagrass biomass. This observation was reinforced by the always positive and usually significant results of the species-species correlation analyses. The mostly positive and significant correlations of shrimp abundances with temperature and/or seagrass biomass suggest that these two factors have a great influence on shrimp population dynamics at Seahorse Key. Bauer (1985) reported no obvious correlation between shrimp abundance and temperature variation in a Puerto Rican Thalassia flat. The temperature range at Seahorse Key (6.7 to 36.7°C), however, was much broader than in Puerto Rico (26 to 31 °C).

Despite the levels of correlation observed between shrimp population patterns, slight separations were seen each year between the peak abundances of Hippolyte

zostericola and the other four hippolytids. These consistently occurring separations fit a pattern that might be explained by density-dependent interactions. Additionally, the unequal distribution of individuals among species in this assemblage fits a pattern that implicates interspecific competition (Huston, 1979) as a potentially important force in controlling the structure of this community.

Community Stability

Stability assessments and the conclusions derived from them depend on monitoring abundance fluctuations in assemblages or communities for periods exceeding by several times the life spans of the assemblage members (Grossman, 1982). The shrimp assemblage at Seahorse Key proved to be ideally suited to meet this longevity requirement. Latreutes fucorum and L. parvulus have been reported (Bauer and Vargas, in press) to have life spans ranging from two to five months. The other hippolytids and the palaemonids at Seahorse Key seem, as evidenced by their size-frequency distributions, to live to similar ages. Thus, if the five month maximum for Latreutes species is used as a typical lifespan, this study encompassed a period exceeding five times the lifespan of the numerically dominant species groups.

All of the methods used to assess stability in this assemblage of species suggested that, despite large fluctuations in the relative and total abundances of each species, it was a resilient community. The use of several analytical techniques which utilized different assumptions

and varying types of data would seem to make this conclusion more robust.

Several authors including Orians (1975), Connell (1978), Grossman (1982), Grossman et al. (1982), and Moyle and Vondracek (1985) have listed characteristics common to resilient and/or persistent communities. Morphological diversity and segregation by habitat and diet are thought to be characteristic of persistent communities. Elastic or resilient communities are characterized by species with short life cycles, with the capacity for high dispersal, with strong migratory tendencies, and with generalized feeding patterns (Orians, 1975). The resilient assemblage of shrimps at Seahorse Key seemed to match the characterisitics of short life spans and capacity for high dispersal (they all have planktonic larval stages). Direct evidence on their migratory tendencies is lacking but migration may account for the virtual disappearance of Periclimenes longicaudatus from the study site after its fall abundance peaks. The resilient structure of the shrimp assemblage at Seahorse Key suggested that deterministic mechanisms, operating within the framework set by temperature and seagrass biomass fluctuations, might be important in controlling individual population abundances within this assemblage.

Grassbed decapods have usually been considered to be virtual ecological equivalents based on assumptions concerning their diets. Generally it has been assumed that they avoid intense food-resource based competition because they all eat detritus which is, in turn, assumed to be a

superabundant resource (Heck and Orth, 1980). Studies of the feeding ecology of grassbed decapods are usually limited to one or two sympatrically occurring species. Only Howard (1984) and Leber (1983) have described the diets of a suite of sympatrically occurring seagrass-bed decapods. Chapter III describes the diets and feeding periodicities and compares the feeding appendages of the caridean assemblage at Seahorse Key. These studies were undertaken to determine if the pattern of generalized feeding behavior predicted by Orians (1975) for species in resilient communities is true of this assemblage. A second purpose was to determine if food-based competition might be an important assemblage-structuring process among these otherwise very similar species.

CHAPTER III
THE TROPHIC ECOLOGY AND FEEDING PATTERNS OF AN ASSEMBLAGE OF CARIDEAN SHRIMPS

Introduction

Decapod crustaceans in seagrass beds are usually trophically classified as either omnivores or detritivores (e.g. Odum and Heald, 1975; Thorp, 1976; Gore et al., 1981; and others). However, recent studies have re-evaluated the trophic status of seagrass meadow-dwelling decapods and have shown that shrimps and crabs are divisible into an array of distinct feeding types (Howard, 1981; Leber, 1983; Kitting, 1984; Orth and Van Montfrans, 1984, Van Montfrans et al., 1984). Detritivory has been found to be much less important and carnivory more important than previously assumed. Earlier ideas concerning the unimportance of food-based interspecific competition among grassbed inhabitants were based on the assumptions that most of these animals ate detritus and epiphytic algae and that these foods were super-abundant resources in seagrass meadows (Heck and Orth, 1980). While detritus is abundant in seagrass beds, its lack of importance in the diets of several sympatrically occurring larger decapods (Leber, 1983) made it essential to assess its role in the diets of the seven small carideans which numerically dominate the shrimp assemblage at Seahorse Key (Vann, 1980;

Chapter II). Diets of these seven species were previously unknown.

After determining shrimp diets by visual analysis of stomach contents it was believed that the degree of resolution in identification of their food types was quite low. Most foods were well macerated and could only be assigned to a few broad categories. Thus, I used SEM photography to compare feeding appendages among all seven caridean species to determine if the dietary similarities which were evident between certain of the seven species were real or if they were a product of the method of analysis. Species-specific morphological differences in feeding structures, for everything from bird beaks (Grant, 1968) to amphipod feeding appendages (Croker, 1967) to radulae of chitons and limpets (Steneck and Watling, 1982), have been used to suggest trophic separation and ecological segregation among sympatric species. It is always possible that dissimilar feeding appendages can be used to collect similar foods and slight differences in feeding appendages can be functionally significant. However, a high degree of similarity in mouthpart morphology coupled with seemingly similar dietary preferences would suggest that these shrimps belong to the same "functional group" (Steneck and Watling, 1982).

Since it seemed likely that all five shrimps in the micrograzer guild at Seahorse Key would have similar diets and microhabitat requirements it was thought that temporal differences in activity patterns could be an important means of resource partitioning among these species. Temporal

partitioning of daily activity rhythms among similar species is the least common type of resource partitioning seen in ecological communities (Schoener, 1974). Crustaceans in open-water habitats, however, have been shown to temporally partition their relatively featureless habitat by showing varying diel patterns of vertical migration. Vertically migrating penaeid shrimps in the open sea, for example, do show some evidence of time-space resource partitioning (Heffernan and Hopkins, 1981).

Howard (1981) pointed out that studies of community structure in marine ecosystems usually neglect behavioral interaction as a mechanism which can determine community structure. Direct observation of most benthic species is, at best, difficult due to the cryptic nature of many animals and to problems inherent in working underwater. Species-specific patterns of feeding activity on diel cycles under field conditions have not been previously described for caridean shrimps from seagrass meadows. I determined patterns of feeding activity by making a series of collections at regular intervals. The collected shrimps were then scored for stomach fullness and species-specific feeding patterns were compared. This technique has been used in other studies involving various animal groups (Heffernan and Hopkins, 1981 for blue-water shrimps; Keast and Welsh, 1967 for lacustrine fishes; and Eberling and Bray, 1976 for kelp forest fishes) where direct observations of animal activities were difficult.

Feeding patterns were thought likely to change from season to season due to changes in seagrass biomass and in the total abundance of shrimp. During summer, shrimp density (Chapter II), seagrass biomass (Chapter II), and predator abundances (Reid, 1954) reach their yearly highs. It was suspected that the patterns of feeding in winter, when all three of these factors reach their lowest levels would differ from the summertime patterns. No predictions were made concerning the type of change which might occur between seasons due to the potential complexity of interactions among these factors. Correlative methods were used to compare feeding patterns among the shrimps.

The resilience observed from year to year (Chapter II) suggested that community dynamics may have been controlled by deterministic (sensu Grossman et al., 1982) processes. According to Grossman (1982) and as listed in Moyle and Vondracek (1985), species within resiliently stable communities should show evidence of trophic specialization. Orians (1975), however, stated that communities which are elastic in response to perturbations (= resilience) should be composed of species showing generalized feeding patterns. Dietary separation is a prediction of Grossman's list of species attributes and dietary overlap seems to be predicted by Orians for the same situation. Results of the stomach content observations were graphically analyzed and overlap values were calculated for all pairs of species in order to examine these conflicting predictions with respect to the Seahorse Key shrimp assemblage.

Methods

Stomach Content Analyses

Cardiac and pyloric stomachs were removed intact, placed on a microscope slide, and teased apart in a drop of 70% ethanol. The alcohol was allowed to evaporate almost completely before the stomach and its contents were covered with mounting medium. A coverslip was placed over the preparation and light pressure was applied to the cover glass to spread the food particles into a thin layer.

Relative proportions of stomach contents were determined by use of a random point technique. An ocular grid, placed over randomly selected fields of view and rotated within the ocular to a random orientation once over each field of view, was used to count the number of times each particle type fell under grid points. Particles counted included organic and inorganic materials. One hundred sixty particles were counted per shrimp stomach. This technique provided data on the approximate percentage by volume (Kitting, 1984) of each particle type in the diets of these caridean shrimps. The number of stomachs examined per shrimp species varied from 14 (Latreutes parvulus) to 25 (Thor dobkini). Records were kept of individual shrimp sizes but the low degree of resolution in identifying stomach contents made attempts to compare diets between seasons and between size groups pointless. All individuals of each species, except Latreutes parvulus, examined in this study were collected on the same date (September 28,

1983). Shrimp abundances, on this day, were near their peak levels during 1983. Due to its generally low abundances L. parvulus were examined from several samples taken before and after this date.

Small, intact prey were occasionally found in the stomachs of Periclimenes longicaudatus and P. americanus. Single stomachs from these two species were sometimes filled by the body of a single prey organism. Thus in addition to estimates of the percent by volume of the organisms, by broad taxonomic categories, the more completely identified prey types are described in the results section.

Values of interspecific food-resource overlap for the seven shrimps were calculated for general food categories by a method of proportional similarity (Schoener, 1970):

$$S = 1 - 1/2 \left[p_{ij} - p_{ih}\right],$$

where p_{ij} = proportion of resource i utilized by species j, and p_{ih} = proportion of resource i utilized by species h. This method provides a measure varying from 1.0 (full overlap between two species) to 0.0 (no overlap).

Feeding Appendage Comparisons

Appendages involved in food acquisition, shredding, and mastication were compared with respect to morphological features which might indicate functional specialization. Photographs were taken of chelipeds, third maxillipeds, and mandibles with a Hitachi ST-1 scanning electron microscope. Photographs were generally limited to the appendage segments expected to be most directly involved in feeding. The

appendages, which were either left attached or removed from the shrimps, were prepared for observation with standard techniques. Shrimps were fixed with either 2% glutaraldehyde in seawater or with 10% buffered formalin in seawater. After fixation the shrimps were dehydrated through an alcohol series. After dehydration they were critical point dried (Denton DCP-1) and sputter coated (Denton Desk-1) for 30-40 seconds at 40 millivolts. Coatings were either gold or gold-palladium. Photographs of appendages were taken at magnifications ranging from 50x to 400x and at acclerating voltages ranging from 5 to 25 kV. An attempt was made to relate observed structural differences and similarities to function and diets using summaries of trends from the carcinological literature. Taxonomic works were also used to establish morphological trends among the segments of appendages which were not included in the set of SEM photographs.

Feeding Patterns

Species-specific patterns of feeding activity on diel cycles were determined by collecting shrimps at two-hour intervals over several days. Two sample sets were collected during distinct periods, several months apart, which differed in shrimp abundances, seagrass above-ground-biomass and mean temperatures (Chapter II). During these seasonally separated periods, samples were collected over three diel cycles spaced at approximately one-week intervals. This protocol was chosen to collect shrimps under a maximum

number of differing combinations of environmental factors, i.e. tidal heights and light intensities.

The epibenthic sled described in Chapter II was towed at slow speed through the shallow Thalassia bed at the main study site. Water temperatures, salinity, depth (cm) at a reference marker, surface light level, and dissolved O_2 were noted after each sled sample. The lengths of sled hauls were not constant but were set by the numbers of shrimps observed in samples taken early on each sampling date. On extremely low tides the sled was pulled by hand.

Shrimp were chilled in ice prior to preservation to prevent regurgitation which reportedly occurs when live shrimp are suddenly exposed to preservatives (Robert H. Gore, pers. comm.). After chilling, collections were preserved with 10% buffered formalin in seawater. Samples were sorted to species. Individuals present in the samples were measured (carapace lengths) and assessed for stomach fullness by use of the following arbitrary scale: 0 = empty, 1 = $<$ half full, 2 = $\geq$ half full, 3 = full and/or distended. Observations on the degree of stomach fullness were aided by clearing shrimps in clove oil. When shrimp tissues became transparent, it was possible to see the outline of each stomach and to estimate its degree of fullness. It was possible, in the smaller individuals of some species, to estimate stomach fullnesses without treatment in a clearing agent. All shrimp included in this study were cleared with clove oil.

Spearmann rank correlation coefficients (BMDP, Dixon, 1983) were calculated between all species pairs. If less than ten individuals of a species occurred in a sample the sample was not included in the analyses. It was thus somewhat difficult to compare the September and February sample sets since several species were either rare in or missing from the winter samples.

Results

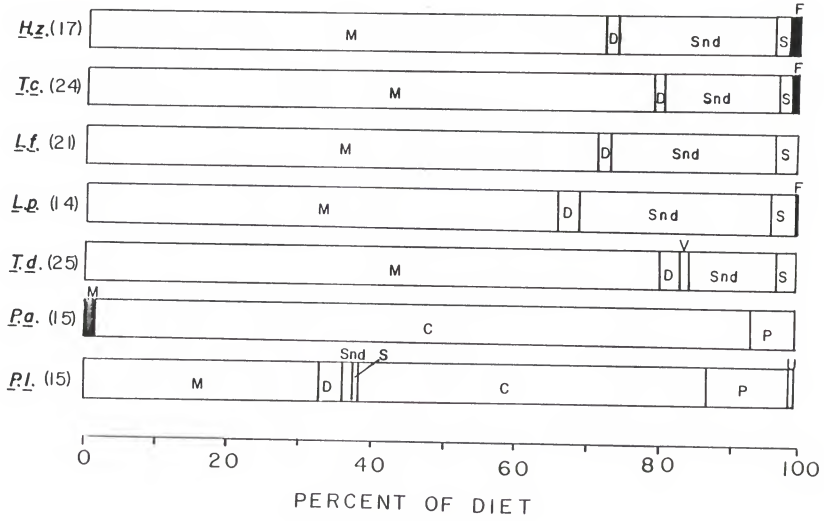
Stomach Content Analyses

Hippolytidae

All stomachs of each of the five hippolytids contained large proportions of well-masticated filamentous microalgae (Figure 3-1). Sponge spicules, crushed diatoms, and sand grains were also commonly present. It was impossible to determine if the sponge spicules were derived from living sponges or from bottom sediments. Most of the diatoms, as judged from the larger fragments, appeared to be centric species. In several cases intact strings of centric diatoms were seen. Sand grains were abundant and were generally free of bacterial growth (as viewed at 400x).

Only the stomachs of Thor dobkini contained identifiable particles of vascular plant tissues. Such particles were found in four of the 25 stomachs examined and thus appeared not to be an important dietary element. A few foraminiferans, which were swallowed intact, were the only evidences of animal consumption by these five shrimps.

Figure 3-1. Diets of seven carideans collected at Seahorse Key. Numbers in parentheses indicate the number of stomachs examined per species. Abbreviations for species are as follows: H.z. = Hippolyte zostericola, T.c. = Tozeuma carolinense, L.f. = Latreutes fucorum, L.p. = Latreutes parvulus, T.d. = Thor dobkini, P.a. = Periclimenes americanus, P.l. = Periclimenes longicaudatus. Abbreviations of items found in stomach contents are: M = filamentous microalgae, D = diatoms, Snd = sand, S = spicules, F = foraminiferans, V = vascular plant detritus, C = crustacean fragments, P = polychaete tissues, U = unidentifiable animal remains.


H.z. (17)
M
D
Snd
S
F
T.c. (24)
M
D
Snd
S
F
L.f. (21)
M
D
Snd
S
L.p. (14)
M
D
Snd
S
F
T.d. (25)
M
D
V
Snd
S
P.a. (15)
M
C
P
P.l. (15)
M
D
Snd
S
C
P
0
20
40
60
80
100
PERCENT OF DIET

Palaemonidae

Unlike the Hippolytidae, the two congeneric palaemonids, Periclimenes americanus and P. longicaudatus, fed primarily on microcrustaceans and polychaetes. The stomachs of P. longicaudatus, however, contained a fair volume of macerated microalgal filaments (Figure 3-1). Diatoms were common but never abundant among the stomach contents of this species. The stomachs of P. americanus contained no sand and only slight traces of very finely divided plant materials. In some preparations it was obvious that the plant materials were originally contained in the stomachs of prey animals. Periclimenes longicaudatus stomachs often contained sand but never in the volumes determined for the hippolytids.

Only a small percentage of the animal tissues observed in the palaemonid stomachs were recognizable beyond a few broad taxonomic categories. Remains of ostracods, copepods and amphipods were occasionally evident amongst the well-macerated tissues. Copepods appeared to have been ingested intact while amphipods were usually cut into large fragments. Polychaete setae embedded in otherwise amorphous masses of tissue were also frequently found in the stomachs of the two palaemonids. Crustacean mandibles were also seen in the guts of both species. Intact foraminiferans and single micromolluscs were sometimes seen in the stomachs of individuals cleared in clove oil but these were not observed in the shrimp stomachs included in the dietary analysis.

Dietary overlap

Interspecific food-resource overlap values (Table 3-1), based on the broad classes of food particles illustrated in Figure 3-1 indicated a high degree of overlap for the five hippolytid species. Evidence for distinct trophic separation was seen only between the two families. Within the palaemonidae the trophic overlap value between the two congenerics was low in comparison to the high overlap values seen within the hippolytidae. The five hippolytids seemed to be almost strictly herbivorous. The masses of filamentous algae seen in their stomachs would indicate that they are micrograzers and not detritivores.

Feeding Appendage Morphology

Mandibles and third maxillipeds

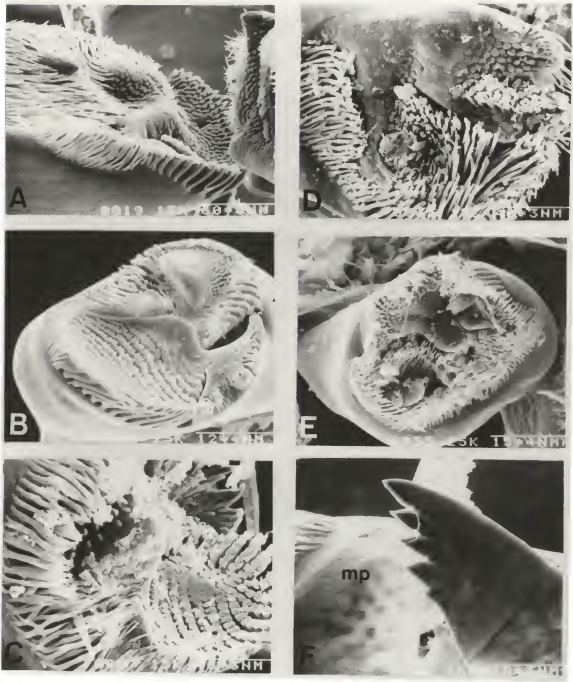
The mandibles of the five micrograzer species are pictured in Figure 3-2. The molar processes of these hippolytid mandibles have both extremely complex patterns of setation and sclerotized knobs and ridges. These hardened surfaces presumably give these shrimps the ability to crush diatom frustules. Figure 3-2a shows the opposing molar processes of Hippolyte zostericola. The mandibular halves are asymmetrical but the hardened ridges on each mandible are opposed by grooves on the opposite member.

The patterns of setation seen on the surfaces of molar processes (Figure 3-2) among these species have not previously been described with regards to their possible functions. The setae on the molar processes pictured here

Table 3-1. Matrix of dietary overlap values calculated as in Schoener (1970). H.z. = Hippolyte zostericola, T.c. = Tozeuma carolinense, L.f. = Latreutes fucorum, L.p. = L. parvulus, T.d. = Thor dobkini, P.a. = Periclimenes americanus, P.l. = P. longicaudatus.

	H.z.	T.c.	L.f.	L.p.	T.d.	P.l.	P.a.
H.z.	1						
T.c.	0.9313	1					
L.f.	0.9765	0.9159	1				
L.p.	0.9242	0.8588	0.9572	1			
T.d.	0.8925	0.9572	0.8919	0.8388	1		
P.l.	0.3740	0.3705	0.3699	0.3838	0.3734	1	
P.a.	0.0000	0.0000	0.0000	0.0000	0.0000	0.4860	1

Figure 3-2. Mandibular processes of the five hippolytids of Seahorse Key. mp = molar process, ip = incisor process. A, Hippolyte zostericola, molar process; B, Tozeuma carolinense, molar process; C, Thor dobkini, molar process; D, Latreutes fucorum, molar process; E, Latreutes parvulus, molar process; F, Hippolyte zostericola, incisor process. Measurements for scale bars are given in nannometers.


A
D
B
E
C
mp
F

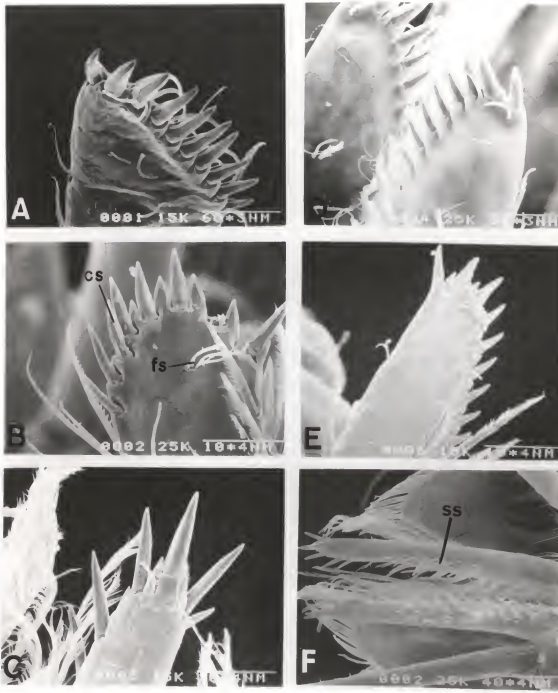
probably function to lift small particles from other mouthparts and to hold the particles in position while they are masticated by sclerotized ridges and patches of blunt nodules. The mandibles of the five hippolytids either have very reduced incisor processes relative to the inflated molariform processes (Figure 3-2f), or lack them completely (Latreutes).

The third maxillipeds of the five hippolytids are similar in that the tips of the appendage, the coalesced propodus and dactylus, are equipped with stout, spine-like, cuspidate setae (Figure 3-3). These setae are set in sockets which lie between spine-like extensions of the palm of the propodus-dactylus. These spines are of varying lengths and shapes but they are present in all five species.

The setae at the tip of the third maxillipeds form claw-like appendages. In Tozeuma carolinense (Figure 3-3b), the tip of the third maxilliped has an arc of cuspidate setae which extend equally down the lateral and medial sides of this pediform cephalic appendage. In the other four species, these spine-like setae continue about equally down the medial side of the propodus-dactylus. There are no stout setae on the lateral border of the terminal segment of these hippolytid species.

Patches of serrate setae (Figure 3-3f) are located below the groups of stout spines on the terminal segments of the third maxillipeds. Smaller and presumably less rigid setae are also present near the tips of the maxillipeds. These flaccid setae bear setules which are neither as

Figure 3-3. Third maxillipeds of the Hippolytidae at Seahorse Key. cs = cuspidate setae, fs = flaccid setae, ss= serrate setae. A, Hippolyte zostericola, tip of propodus-dactylus; B, Tozeuma carolinense, palm of propodus-dactylus; C, Thor dobkini, palm of propodus-dactylus; D, Latreutes fucorum, palm of propodus-dactylus; E, Latreutes parvulus, palm of propodus-dactylus; F, Thor dobkini, shaft of propodus-dactylus showing position of serrate grooming setae. Measurements for scale bars are given in nanometers.

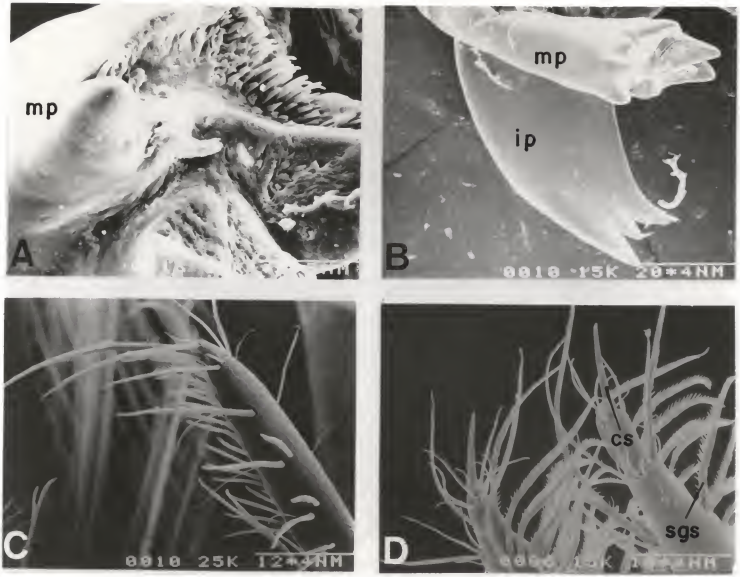

A
cs
fs
B
E
C
SS
F

numerous nor as stout as the setules seen on the serrate setae.

Mandibles of the two palaemonids were stikingly different than those of the micrograzers (Figure 3-4a and b). Periclimenes longicaudatus has a large incisor process (not pictured) and small patches of setae can be seen on the crushing surfaces of their molar processes (Figure 3-4a). This combination of a large incisor process and a molar process with some setation agrees with the omnivorous feeding habits of P. longicaudatus. Periclimenes americanus has a ventral incisor process which is nearly as large as its molar process (Figure 3-4b). The molar processes of this shrimp completely lack setae. The appearance of the molar process suggests that its entire surface is hardened and functions as a crushing or cutting surface.

The third maxillipeds (Figure 3-4c and d) of both species of Periclimenes considered in this study are morphologically distinct from those of the five hippolytid species. A single terminal setal spine (Figure 3-4d) replaces the groups of stout, cuspidate setae seen in the hippolytidae. The terminal segment of this appendage in these two species are densely covered with strong serrate setae. Long serrate setae are especially prominent on the terminal segment of P. americanus (Figure 3-4d). In P. longicaudatus the setae of the propodus-dactylus (Figure 3-4c) seem shorter than than those of P. americanus. In both species the setae are set in sockets. A few flaccid

Figure 3-4. Mandibles and third maxillipeds of two Palaemonids from Seahorse Key. mp = molar process, ip = incisor process, cs = cuspidate setae, sgs = serrate grooming setae. A, Periclimenes longicaudatus, isolated molar process showing teeth and patch of setae; B, Periclimenes americanus, molar and incisor processes; C, P. longicaudatus, tip of third maxilliped; D, P. americanus, tip of third maxilliped showing terminal cuspidate setae and position of serrate grooming spines. Measurements for scale bars are given in nannometers.


mp
A
mp
ip
B
0010 25K 20+4NM
C
0010 25K 12+4NM
cs
sgs
D

setae, which are also somewhat serrate in form, are mixed in with the stronger serrate setae.

Chelipeds

The second chelate pereiopods of all five hippolytids have annulated carpi (a taxonomic characteristic) and possess chelae which are lighter than those of the first pereiopods. On both the first (Figure 3-5) and second pereiopods (Figure 3-6) of these micrograzers the chelae are surrounded by dense patches of flaccid setae. These setae are more abundant on the propodus-dactylus of the second cheliped than they are on the corresponding segment of the first cheliped.

The chelae of the first and second pereiopods possess stout terminal setae which interlock when the chelae are closed. The cuspidate terminal setae of the first chelipeds of Tozeuma carolinense are unique among these five hippolytids in that they possess small tooth-like setules (Figure 3-5b and f). The cuspidate setal spines of the other four species lack these setules.

The chelae of the first pereiopods of these five species showed no great differences in structure. The only noticeable difference involved the cutting surfaces of the first chelae. In Hippolyte zostericola (Figure 3-5a) the opposing surfaces of the propodus and dactylus bear small teeth. Latreutes fucorum (Figure 3-5d) lacks these teeth. The dactylus of L. fucorum's first pereiopod appears to fit into a scoop-like depression in the apposing propodal

Figure 3-5. First periopods of the Hippolytidae of Seahorse Key. cs = cuspidate setae, d = dactylus, p = propodus, fs = flaccid setae. A, Hippolyte zostericola, tip of cheliped showing dentition along opposing edges; B, Tozeuma carolinense, tip of cheliped showing terminal cuspidate setae and flaccid, chemosensory setae; C, Thor dobkini, tip of cheliped; D, Latreutes fucorum, tip of cheliped; E, Latreutes parvulus, tip of cheliped; F, L. parvulus, end on view of cheliped showing scoop-like surface of the propodus. Measurements for scale bars are given in nannometers.

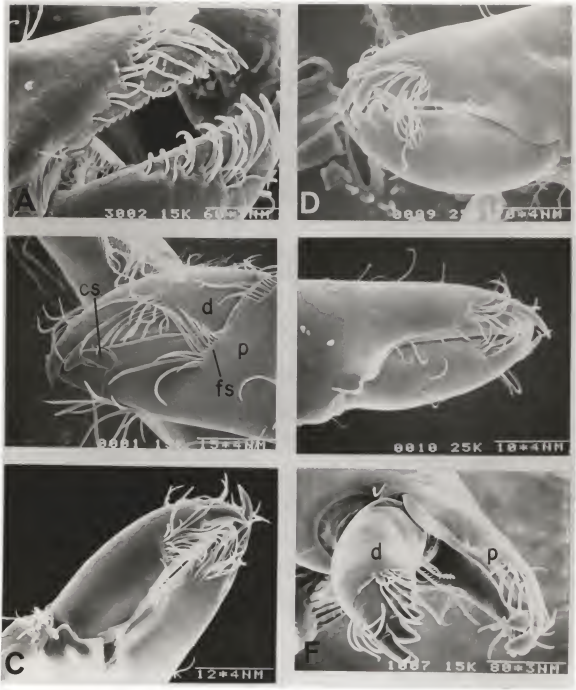
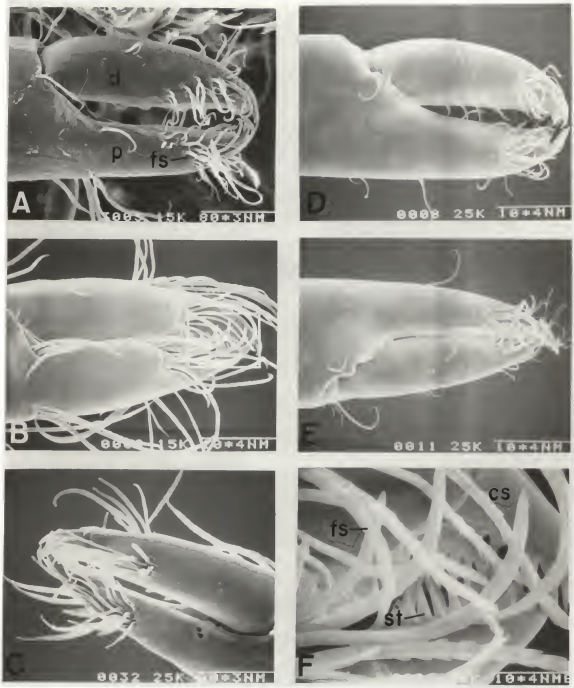

A
D
cs
d
p
fs
C
F
d
p

Figure 3-6. Second pereiopods of the Hippolytidae of Seahorse Key. cs = cuspidate setae, d = dactylus, fs = flaccid setae, p = propodus, st = setules. A, Hippolyte zostericola, tip of cheliped ; Tozeuma carolinense, tip of cheliped (boxed area enlarged 5X in F); C, Thor dobkini, tip of cheliped; D, Latreutes fucorum, tip of cheliped; E, Latreutes parvulus, tip of cheliped; F, Tozeuma carolinense, cuspidate setae with setules from boxed area in B. Measurements for scale bars are given in nannometers.


d
p
fs
A
D
25K
B
E
0011 25K
cs
fs
st
C
F

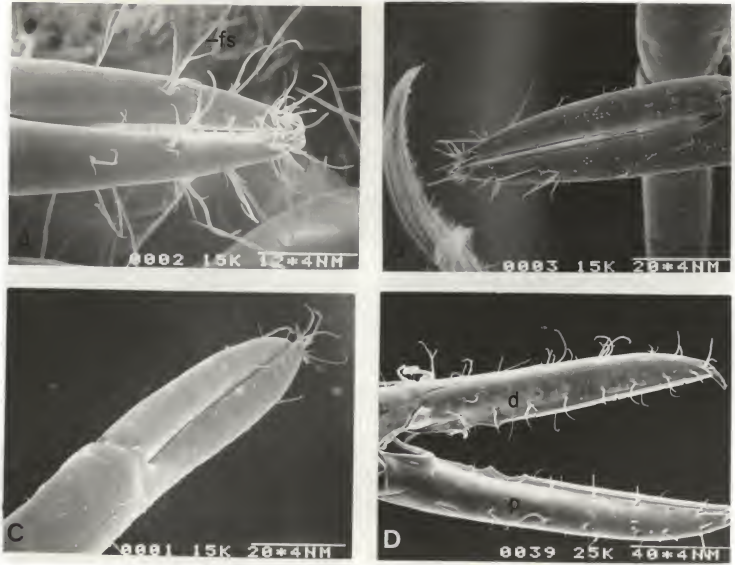
surface. The first cheliped of Thor dobkini (Figure 3-5c) appears to be similar in this respect. The chelae of the other two species also seem to have propodal depressions in which the dactyli rest when the chelae are closed. Their opposing edges were not seen because very few individuals were found with chelipeds in an open position. Numerous attempts to open these tiny claws resulted in their destruction. Thus it was not determined if their opposing edges bore teeth.

In all five species the opposing surfaces of the second pereiopods' propodus and dactylus (Figure 3-6) lack teeth. The dactylus of the second pereiopod of Latreutes fucorum rests in a spoon-like depression in the opposing propodal surface (Figure 3-6d).

As is true of the mandibles and third maxillipeds the chelipeds (Figure 3-7) of the two palaemonids also differ considerably from the same appendages of the hippolytidae. The second chelipeds of the palaemonidae are longer and more robust in comparison to their first chelate pereiopods. The carpus of the second chelipeds is not annulated which greatly reduces its flexibility. In Periclimenes longicaudatus and americanus both sets of chelae have patches of distally located flaccid setae similar to those seen in the hippolytidae.

The propodi of the first and second chelate pereiopods of both species lack the spoon-like depression and teeth seen in the hippolytidae. Instead dactyli and propodi of the first and second chelate pereiopods (Figure 3-7), in

Figure 3-7. First and second pereiopods of Periclimenes longicaudatus and P. americanus. d = dactylus, p = propodus, fs = flaccid chemosensory setae. A, P. longicaudatus, tip of 1st pereiopod, lateral view; B, P. americanus, tip of 1st pereiopod, lateral view; C, P. longicaudatus, dactylus and propodus of 2nd pereiopod; D, P. americanus, tip of 2nd pereiopod with chela in open position. Note single cuspidate seta at tip of dactylus and low tooth-like notches near junction of the dactylus and propodus. Measurements for scale bars are given in nannometers.


fs
0002 15K 12*4NM
0003 15K 20*4NM
C
0001 15K 20*4NM
d
p
D
0039 25K 40*4NM

both species, have long, thin, blade-like opposing edges. The palms and movable fingers of the two palaemonids have a stout terminal spine (Figure 3-7d) which may guide the two segments into the proper alignment when the chelae close. Several teeth can be seen (Figure 3-7d) near the junction of the propodus and dactylus of the open cheliped of P. americanus.

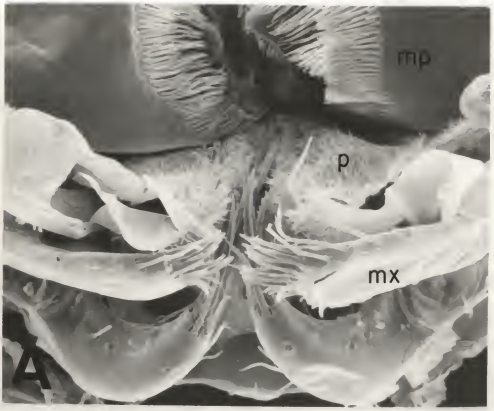
Other feeding appendages

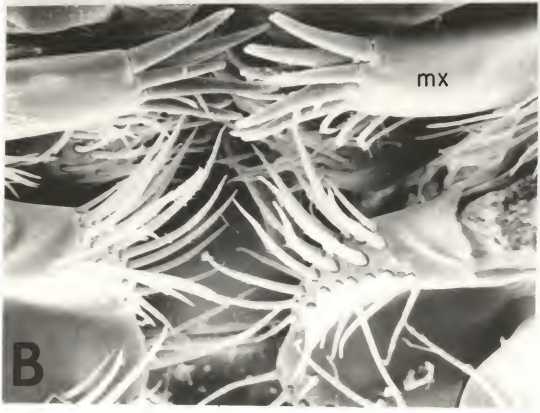
Figures 3-8a and 3-8b show the cephalic appendages which lie below the mandibles of Latreutes parvulus and Periclimenes americanus, respectively. The maxillules of both species possess stout, spine-like setae at their tips. These setae function to transfer small particles to the mandibles and to hold larger particles while they are processed by the mandibles. The endites of the maxillae presumably serve to pass food to the mandibles. These appendages appear to be very similar in structure despite the fact that one species is a carnivore (P. a.) and the other species is a herbivore (L. f.).

The other thoracic appendages, the first and second maxillipeds, of these seven species are primarily involved in food transfer and the production of water currents. While they are important in the feeding process, they were assumed not to limit feeding patterns by affecting food selection and/or its processing prior to ingestion.

The non-chelate pereiopods of these species may play a role in food location. They are equipped with setae which

Figure 3-8. Cephalic appendages beneath mandibles. mp = molar process, mx = maxillule, p = paragnathal flap. A, Latreutes parvulus, shows relationship of maxillules to the molar process; B, Periclimenes americanus, shows maxillules and maxillae beneath molar process.


mp
p
mx
A


mx
B

may be chemosensory in function and they can pass food particles to the other feeding appendages. They were, however, assumed not to have a great influence on the overall trophic status of these seven species.

Feeding Patterns

Means of temperature and salinity based on data taken during the two months included in the feeding periodicity study are given in Table 3-2. Seagrass biomasses and total shrimp densities as observed during regular monthly collections (Chapter II) are also shown in this table. Seagrass biomass data from September 1983 are given because seagrasses were not sampled quantitatively in September 1982. Judging from qualitative observations this biomass figure probably represents a close approximation of the above-ground-biomass at the time of the 1982 sampling. Table 3-2 shows marked differences, with the exception of salinity, in each of the included factors between the September and February sample sets.

Feeding activity patterns of a subgroup of the seven species were examined for correlations with one another by Spearman rank correlation statistics. The hemimatrices in Tables 3-3 and 3-4 present the results of correlation analyses from data collected in September and February, respectively. Positive and significant correlations were found between four of six possible pairings (Table 3-3) in the September samples. During February two pairings (Table 3-4) produced positively significant correlations.

Table 3-2. Mean values of temperature, salinity, seagrass biomass, and shrimp density during sampling periods included in the feeding periodicity study. As explained in the text the September 1982 seagrass biomass value was taken from data collected during September 1983.

Month	°C	°/oo	Total density	Seagrass biomass
September 1982	28.6	32.9	331.9	138.3
February 1983	17.8	33.2	65.6	16.9

Table 3-3. Spearman rank correlation matrix of species-specific feeding intensity patterns. Samples taken during September 1982. N = 23. The lower hemimatrix gives r_s values and the upper hemimatrix illustrates significance levels for each pairwise comparison.

	H.z.	*T.c.*	*L.f.*	*L.p.*
H.z.	1	n.s.	**	n.s.
T.c.	0.283	1	*	**
L.f.	0.614	0.399	1	**
L.p.	0.322	0.734	0.583	1

N.S. $P > 0.05$
* $P < 0.05$
** $P \leq 0.01$

Table 3-4. Spearman rank correlation matrix of species-specific feeding intensity patterns. Samples taken during February 1983. N = 19. The lower hemimatrix gives r_s values and the upper hemimatrix illustrates significance levels for each pairwise comparison.

	H.z.	T.c.	L.f.	L.p.
H.z.	1	*	n.s.	n.s.
T.c.	0.517	1	n.s.	*
L.f.	0.131	-0.301	1	n.s.
L.p.	0.391	0.525	-0.141	1

N.S. $P > 0.05$
* $P \leq 0.05$
** $P \leq 0.01$

Discussion

Dietary Similarities

The five hippolytid species collected from the Thalassia beds adjacent to Seahorse Key were found to have similar diets in that filamentous microalgae and diatoms were present in abundance in the stomachs of each of these species. There are many species of epiphytes on Thalassia blades as evidenced by the species lists of Thursby (1976) and Humm (1964). Kitting (1984) demonstrated, using in situ photographic methods, that micrograzing snails in seagrass beds have definite preferences for certain microalgal species. He also described the progression of epiphytic succession on Thalassia blades. This sequence begins with diatoms settling first on new blade surfaces. Diatoms are followed by filamentous algae which are then replaced by coralline algae. These same trends are apparent from seasonal collections of Thalassia epiphytes as reported by Thursby (1976) at Seahorse Key. Fosiella atlantica, a coralline species, became numerically dominant during the late fall and early winter. The coralline species are tougher (Steneck and Watling, 1982) and are presumably less palatable to most micrograzers. Thus while microalgae may seem abundant in seagrass beds not all species are of equal nutritional quality. They also provide an assortment of morphological types, based on size, toughness, and composition, on which micrograzers could specialize. Micrograzers have also been

shown to be capable of limiting the growth of epiphytes on seagrass blades (vanMontfrans et al., 1984).

Due to the well-macerated condition of the algal filaments and diatoms it was not possible to visually determine if these shrimps fed selectively on the array of available microalgal species. It was possible to distinguish between algal tissues and detritus derived from vascular plants. At high magnifications (250 to 400x) cell walls were visible in particles of vascular plant detritus. These particles also seemed to be less finely divided than the fragments of filamentous microalgae.

Vascular plant detritus was found to be unimportant in the diets of the seven carideans included in this study. Definitely identifiable fragments of vascular plant tissues were seen only in the stomach contents of Thor dobkini. Detrital particles occurred in only four of the twenty-five T. dobkini examined and accounted for less than one percent of its diet. The apparent rarity of detrital particles in hippolytid diets agrees with similar studies of other grassbed-inhabiting decapod crustaceans. In Apalachee Bay, Florida, Leber (1983) found detritus to be generally unimportant in the diets of 14 species of crabs and large shrimps. Howard (1984) reported that almost 70% of the food consumed by Hippolyte caradina was "plant detritus" but he also stated that recognizable fragments of macrophyte tissues were not detected. As pointed out by Kitting (1984), authors who have reported the ingestion of large amounts of

detritus by seagrass bed animals have generally used relatively low magnifications when viewing stomach contents.

At Seahorse Key the two small, congeneric palaemonids, Periclimenes americanus and P. longicaudatus, had diets which did not greatly overlap with each other or with the five hippolytid species. P. americanus was found to be a strict carnivore while P. longicaudatus was an omnivore. Animals taken as prey by these two species were usually well macerated and were usually recognizable to only very broad taxonomic categories. Occasionally, fragments of amphipods, copepods, and ostracods were seen. Single micromollusks or large foraminiferans were sometimes seen intact within cleared stomachs but were not observed in the set of stomachs microscopically examined to determine their contents. Polychaete setae were often encountered in the stomachs of these two species.

In addition to animal tissues, Periclimenes longicaudatus ingested considerable quantities of microalgae. If present, detritus derived from vascular plants was not evident. Morgan (1980) found that a slightly larger palaemonid species, Palaemonetes pugio, in Texas Halodule beds consumed attached epiphytes and small crustaceans and ignored seagrass tissues. He noted, as reported elsewhere in the literature, that the diet of this wide-ranging species varies considerably depending on habitat types and the foods available. The diets of P. longicaudatus and P. americanus have not previously been described so it is impossible to say if their diets also vary with location.

Reduced gastric mills consisting of a single median tooth and a median set of ossicles are characteristic of the hippolytidae (Patwardhan, 1954; Coombs and Allen, 1978). Sand plays a role in the trituration of food particles, thus replacing some of the functions of the gastric mill of Hippolyte varians (Coombs and Allen, 1978). The amount of sand reportedly increases in the cardiac stomach of this omnivorous species when it feeds heavily on plant materials. Sand grains and spicules were abundant in the stomachs of H. zostericola and in the stomachs of the other four hippolytid species. Inorganic particles were present but less abundant in the stomachs of the omnivorous Periclimenes longicaudatus. No sand grains were seen among the stomach contents of P. americanus. The large amounts of sand seen in the stomachs of the hippolytids at Seahorse Key provides additional evidence that these species are true herbivores but does not help in determining the origin of the ingested plant materials.

Diel patterns of change in caridean abundances in seagrass meadows also suggest that these animals are micrograzers and are not detritivores. Kitting (1984) found that most micrograzers, including a penaeid shrimp, move upwards on seagrass blades at night to feed. If detritus were an important dietary component, then these animals would be expected to remain near the sediment surface at the bases of seagrass plants. Several authors have demonstrated that seagrass bed dwelling decapods are easier to catch, and thus seem more abundant, at night (Howard, 1981; Greening and

Livingston, 1982; Bauer, 1985). Presumably this is at least partially due to changes in position on seagrass plants related to increased feeding activity. Densities of the hippolytids and the small palaemonids found at Seahorse Key and throughout the shallow waters of the northeastern Gulf of Mexico, follow this same diel rhythm of change (Greening and Livingston, 1982; personal observation).

Feeding Appendage Morphology

The low level of resolution in identifying food particles from the stomachs of these carideans made it necessary to validate dietary observations by some other means. Immunological techniques (i.e. Marshall, 1977; Feller et al., 1979) could have been used to identify more consistently food types in gut contents to lower taxonomic levels than those determined by visual techniques. The slight increase in resolving power (usually to the familial level) that might have been achieved by serological methods would still not permit one to determine if the hippolytids were specializing on different species of microalgae. Serological techniques also do not permit one to determine the quantity of each food type identified in the gut of a tested animal.

Comparisons of feeding appendage morphology were undertaken to identify specialized functional groups, if they existed, among the small carideans at Seahorse Key. Bauer (1975, 1977, and 1978) and Fryer (1977) have described feeding structures and their multiple roles in feeding and grooming for a wide variety of carideans. These studies of

functional morphology and drawings of shrimp appendages in the taxonomic literature were used to make inferences concerning the usages of the feeding appendages of the Seahorse Key carideans. As mentioned in Factor (1982) it is extremely difficult to make accurate line drawings of the complex mouthparts, especially the mandibles, of decapod crustaceans. Most figures, with a few notable exceptions (especially Fryer, 1977) do not adequately show the complex patterns of setation and dentition which are characteristic of shrimp appendages. For this reason SEM photographs were used to make general comparisons of the feeding appendages most likely to be directly involved in food collection and/or processing. Only mandibles, third maxillipeds, and chelate pereiopods were compared as these are the appendages which would most directly limit the selection of food types. Other mouthparts are largely involved in guiding and transferring food particles to the mandibles (Farmer, 1974; Fryer, 1977; Coombs and Allen, 1978).

As an adaptation to grooming, hippolytid second pereiopods tend to be well equipped with strong serrate setae on their various segments (Bauer, 1978; Howard, 1981). Patches of smaller, less robust setae can be seen near the tips of the second chelipeds of all the hippolytids considered in this study. These setae are serrate but appear to be less rigid than those known to be involved in grooming. These setae match the general description of setal types known to have chemosensory functions (Factor, 1978; Howard, 1981).

Hippolytid second pereiopods function in food collection but they tend to be slender and less robust in comparison to their first chelipeds. The first chelipeds lack dense patches of serrate setae and are less limber than the second pereiopods. Within the hippolytid family the chelae of the first pereiopods are primarily used in the collection and maceration of foods (Bauer, 1978; Coombs and Allen, 1978).

The chelae of the Seahorse Key hippolytids follow patterns similar to those described in the literature. In all five species the second cheliped is more slender than the first. The opposing surfaces of the chelae of the first two pereiopod pairs are generally similar in shape. In each species except Hippolyte zostericola, dactyls fit into a spoon-shaped depression on the opposing propodal surfaces. The chelae are also characterized by several interlocking cuspidate setae located at the distal tips of the propodus and dactylus. The opposing dactylar and propodal surfaces of the first cheliped of H. zostericola were unique in that they posessed many small tooth-like denticles. Latreutes fucorum and Thor dobkini lacked these denticles. In these species the sharp edges of the propodal depressions may grasp and cut large food particles before they are transferred, within the propodal scoop, to the the more anterior mouthparts.

In Tozeuma carolinense the cuspidate interlocking setae were found to be finely toothed while these setae in the other four hippolytids were smooth. The functions of these

teeth-like setules are unknown. Despite differences in the overall morphology and size of these five species, their chelipeds were similar in structure and, presumably, in function.

The robust serrate setae seen on the third maxillipeds of hippolytids and other carideans are primarily used in antennular grooming (Bauer, 1977) and in cleaning the other mouthparts (Coombs and Allen, 1978). The large cuspidate setae on the tips and medial borders of the coalesced propodus-dactylus function in the manipulation of large food particles. Food morsels too large for cheliped cutting edges may be passed to the third maxillipeds and shredded between these spines and/or sliced apart by the mandibular cutting surfaces (Coombs and Allen, 1978). Among the Seahorse Key hippolytids these cuspidate setae were generally found to be similar in overall shape and location. The arrangement of these terminal setal spines in Tozeuma carolinense was slightly different than seen in the other four micrograzer species. This difference in pattern may or may not have been functionally important. T. carolinense were found in greatest numbers within patches of Syringodium filiforme, a round-bladed seagrass. Perhaps the bear claw-like setal arrangement, instead of indicating a functional difference, was an adaptation of this species associated with feeding on microalgae scraped from a curved substratum. The difference in pattern may also have been related to grooming the elongate body of this uniquely shaped species.

The mandibles of the five hippolytids were found to be very similar in form and thus, were also presumbaly similar in food processing capabilities. The incisor processes of these species were either small or lacking. Molar processes within this family were much more prominent. A large molar process is typical of microphagous species (Fryer, 1977).

In the Atyidae, a family of freshwater carideans, the molar processes have ridged surfaces (Fryer, 1977) but do not have the complex patterns of setation seen here in the Hippolytidae. The exact functions of these setae are impossible to observe since the mandibles lie above the more ventral mouthparts and behind the paragnathal flap. It is assumed here that the setae and their setules function to sweep particles from the other mouthparts and to hold these particles in the proper position during mastication. After mastication, food particles on the mandibles are swept towards the opening of the esophagus (Fryer, 1977) by the rolling movements typical of crustacean mandibles (Manton, 1977).

Howard (1981) observed crushed diatom frustules on mandibular surfaces in Hippolyte caradina. Such particles were not seen in this study because all feeding appendages were sonically cleaned several times during the dehydration process.

The mandibles, third maxillipeds, and chelate pereiopods of the Hippolytidae were very similar in structure and presumably in function. These morphological observations and the high levels of dietary overlap in all pair-wise

comparisons among the Hippolytidae indicate that these species are trophically similar and that they should be considered members of the same functional group.

The same sets of structures observed in the two carnivorous palaemonids were strikingly different. The chelipeds of Periclimenes americanus and P. longicaudatus are more slender and lack the spoon-shaped depressions characteristic of the hippolytid chelipeds. Instead, long, thin blade-like edges are present on the opposing dactylar and propodal surfaces. Additionally, the dense patches of setae seen in the Hippolytidae are absent in the two palaemonids. Their cheliped setae are also short and flaccid but they are widely scattered across the surface of the chela. They too have characteristics of setae known to have chemosensory functions in lobsters (Farmer, 1974; Factor, 1978). The opposing tips of the chelae of these two congeneric shrimps are each equipped with single cuspidate setae. These single spines may function to guide the closing dactylus into the proper position relative to the propodal blade (Bauer, 1978). Several teeth can be seen near the juction of the propodus and dactylus on the interior surface of the open cheliped of P. americanus. Such teeth may function to more securely grasp captured prey.

Chelipeds of the Palaemonidae lack the annulated segments characteristic of the carpus of the hippolytid second pereiopod (Chace, 1972). Thus, the second chelipeds of Periclimenes americanus, P. longicaudatus, and other palaemonids are relatively rigid and play a lesser role in groom-

ing general body surfaces (Bauer, 1978). The first chelipeds and the rest of the walking legs of palaemonids are involved in cleaning exoskeletal surfaces whereas the second cheliped pair are used most often in feeding.

The third maxillipeds of the two palaemonids are distinctly different in overall configuration than those of the five hippolytids. Many long, serrate setae are apparent on the maxillipeds of Periclimenes americanus. The serrate setae of P. longicaudatus are less numerous and quite short in comparison to those of P. americanus. In both species, however, the serrate setae of the third maxillipeds are in similar locations and can be assumed to have similar functions. Caridean antennules, especially their patches of olfactory aesthetascs, are frequently cleaned by these brushes of serrate setae (Bauer, 1975; 1977). Other appendages are also cleaned by the third maxillipeds.

Food handling would seem to be a secondary function of palaemonid third maxillipeds. Unlike the hippolytids found at Seahorse Key, the third maxillipeds of Periclimenes americanus and P. longicaudatus are not equipped with numerous cuspidate spines at their tips. Instead, the tips of the palaemonid third maxillipeds bear a single, long terminal spine. The single spine may be used to hold prey close to the more anterior mouthparts as described for similar structures in the Penaidae (Alexander et al., 1980).

Mandibles of the Seahorse Key palaemonids are also shaped much differently than those characteristic of the five hippolytids. Incisor and molar processes of nearly

equal size are evident on the mandibles of P. americanus. Although not shown here the incisor processes of P. longicaudatus (drawn in Holthuis, 1952) are similar in relative size and shape to those of P. americanus. The incisor process of P. americanus has three sharp teeth which are undoubtably used in cutting pieces from large prey. The mandibular process of P. americanus completely lacks surface setation. Instead it is equipped with six heavily sclerotized and rounded teeth. The teeth surround a large central depression. These surfaces can probably be used either as crushing or cutting surfaces. The molar process of the omnivorous P. longicaudatus has a small patch of setae and three large teeth. The setae are smooth in comparison to the highly setulated setae of the five hippolytids. Despite these differences in texture and size, they may also be used to hold small food particles in place and/or to sweep masticated food materials towards the esophagus. This mixed configuration of large sclerotized teeth and reduced setation seems to be precisely reflected in the omnivorous feeding habits of P. longicaudatus.

In summary, the appendages most likely to be directly involved in feeding by the seven small carideans are similarly constructed within families but are strikingly different between families. These major morphological differences are reflected in the diets of each group. All of the hippolytids are micrograzers while the two palaemonids are at least partially carnivorous in their feeding habits.

Within the Hippolytidae there was no strong evidence of morphological differences which might have been indicative of feeding specializations. The presence or absence of a mandibular incisor process seemed to be the strongest evidence for trophic specialization. Hippolytids with incisor processes might be capable of eating larger and/or tougher microalgae than would be true of species without such structures. Other minor differences were evident but were assumed not to greatly influence feeding capabilities.

An important conclusion to be drawn from this investigation is that these species are not detritivores. As mentioned in the introduction, many seagrass meadow decapods previously have been assumed to include much detritus in their diets. As was true of the larger decapods in nearby Apalachee Bay (Leber, 1983), these small shrimps cover a range of trophic levels. Thus, earlier ideas concerning the unimportance of food-mediated interspecific competition, which were based on the assumed importance of detritus as a super-abundant resource in the diets of seagrass dwellers, need to be reassessed with regards to seagrass bed decapods.

Temporal Separation

High levels of nocturnal activity have been widely reported for most shrimp species (Howard, 1981; Greening and Livingston, 1982; Bauer 1985). Four species of shrimps from Australlian grassbeds were observed, in aquaria, to have different activity levels during day and night (Howard, 1981). These shrimps were generally inactive or engaged in

non-locomotory activities during day and were more mobile at night. Night-time locomotory activities included swimming, walking, and feeding. Bauer (1985) reported similar activity patterns for Latreutes fucorum, L. parvulus, and Hippolyte curacaoensis held in tanks. These species were found to be permanent residents on seagrass blades. These shrimps were inactive during the day and swam between or moved about on seagrass blades at night. Association of seagrass bed hippolytids with seagrass blades seems to be the general case (reviewed by Kikuchi and Peres, 1977). These small species do not burrow into bottom sediments. Higher abundances of shrimps in night-time grassbed samples (Greening and Livingston, 1982; Bauer, 1985) are therefore probably a result of shrimps being easier to catch, in trawls and other sampling devices, while they are moving about.

The complete lack of negative correlations and high number of positive significant correlations between activity patterns of the most abundant micrograzers as observed in September provided evidence that these species had similar patterns of feeding activity. Thus temporal differences in feeding behavior patterns did not seem to be an important method of resource division in this grassbed community. The statistically similar patterns of activity may have indicated the presence of a mutually safe feeding period for the micrograzer species.

It is tempting to speculate that the similarities in feeding patterns seen near peaks in total abundance may have

produced intense interspecific interactions. In seagrass beds Palaemon floridanus can displace the less aggressive Palaemonetes vulgaris (both species are small palaemonids) from their mutually preferred habitat of algal masses (Coen et al.,1981). Individuals not associated with dense vegetation were found to be more susceptible to predation. Thorp (1976) also found that interspecific aggression between Palaemonetes vulgaris and Palaemonetes pugio produced field observed patterns of spatial separation. While these two species are slightly larger and are morphologically quite different than members of the Seahorse Key caridean assemblage the earlier study suggests that preferred microhabitats can be limiting in seagrass beds. Vann (1980) found evidence of habitat separation between Hippolyte pleuracantha (= H. zostericola at Seahorse Key) and Tozeuma carolinense but saw no evidence of aggressive interactions when both species were held together in an aquarium. The behavior of these species is presumably greatly altered by aquarium environments. There were observable differences in the field distributions of each of the seven caridean species (Chapter II), however, this was not a long-term focus of this study.

If the micrograzer species are not specialized for different microalgal species, which is suggested by the very similar morphologies of their feeding appendages, then food based competition might be an important process which could contribute to the level of stability observed in this assemblage of shrimps. Competition for sufficient amounts of

epiphytic algae, the major item in the diets of the micrograzers, in "enemy-free space" (Jeffries and Lawton, 1984) could have produced detectable differences in patterns of temporal partitioning. However such differences were not observed during September when shrimp densities peaked in 1982. Considering the high level of predation intensity, which has been shown to have a strong influence on seagrass-bed community structure (reviewed in Chapter I), competitive interactions, in several forms, between the hippolytids may have resulted in a second outcome. Competitive displacement of individuals from protective feeding sites, containing adequate amounts of microalgae, during mutually "safe" feeding periods, could have contributed to the resilient structure seen from year to year (Chapter II) in this seagrass community. Competition among these similarly sized species for protective refuges during the day could also have played a large role in structuring the assemblage. Local extinction of the less abundant species would not occur because of recruitment to this grassbed from distant populations and because of the yearly seagrass dieoffs which set the structure of this grassflat assemblage back to an earlier successional state. Thus competition (including food-based competition), predation, and environmental parameters might interact to control the structure of this shrimp assemblage.

CHAPTER IV

CONCLUSIONS AND RECOMMENDATIONS FOR FURTHER RESEARCH

All of the methods used to assess the stability of this assemblage suggested that it was resilient following large natural disturbances in community structure. The use of several analytical techniques, which were based on different assumptions and which used differing combinations of data types, would seem to make this conclusion more robust. The primary problem with all of these techniques seems to be their susceptibility to bias. The Bloom method of stability analysis seems to be the most objective technique of stability assessment currently available. It circumvents some possible sources of bias by utilizing the entire range of data types available in a species by collection date data matrix.

Stability in communities presumably results from various non-stochastic, interactive processes between species which set community or assemblage structure. The seven species considered in this study each possessed unique combinations of traits (e.g., Hippolyte and Tozeuma consumed large amounts of microalgae but had differing patterns of distribution across seagrass beds) which could result in reducing niche overlaps between species and could be important in determining community structure. The ecological

significance of each set of species-specific traits would be extremely difficult to determine.

As discussed in Chapter III interspecific competition for food among grassbed fauna has usually been assumed to be avoided by the consumption of detritus. In this study only one of the seven species considered contained identifiable fragments of detritus in its stomach contents. Even in this one species the amount of detritus seemed negligible in comparison to the masses of epiphytic microalgae present in most stomachs. Observations on feeding selectivity and monitoring seasonal changes in epiphyte abundance would be required to determine if food-based competition is an important community-structuring process among grassbed decapods. However, contrary to the earlier assumptions and in agreement with other recent observations on seagrass-bed decapods, such interactions are not avoided by community-wide consumption of detritus.

From the similarities in body size, diets, feeding structures, and diel feeding patterns seen among the Hippolytidae it seems likely that the population sizes of these generally abundant species may be influenced by interspecific competition. The uneven distribution of individuals among these species and the separation of seasonal peaks in their abundance patterns provided additional evidence which supports this hypothesis. Obviously this is circumstantial evidence and it needs to be verified by field manipulation of the various species' populations. Such

experiments, however, are notoriously difficult to perform in grassbed communities.

Investigators contemplating manipulative field experiments to test hypotheses concerning population interactions in seagrass beds with carideans and other small species should be aware of some of the problems they may encounter. Experiments based on caging techniques, in order to include or exclude certain species, are at best difficult to conduct without creating a high level of artificiality. The small adult size of the hippolytids and palaemonids require cages constructed with small mesh-sizes in their side panels. Exclusion of planktonic larval stages and small post-larvae of most carideans would require side panels constructed of 500 micron mesh. In addition to restricting water exchange and decreasing light intensity small-meshed side panels provide an excellent substratum for algal fouling. Scrubbing the cage sides would fertilize the micrograzers with a rain of their favorite foods. It is also extremely difficult to exclude or include the many highly mobile, and sometimes burrowing, predators found in seagrass beds. Natural experiments, despite their inherent problems, and close observation of species characteristics, seem to be the best tools available in characterizing the nature of structural regulation of assemblages of small animals in seagrass meadows.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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